The Role of Advance Growth in Upland Rainforest Restoration, Pohnpei, Federated States of Micronesia

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Abstract

Upland tropical rainforest on Pohnpei island, Federated States of Micronesia, declined from 42 % of land area in 1975 to 15 % in 1995, largely through conversion to sakau (*Piper methysticum* G. Forst.) cultivation. As part of a research programme aimed at restoring degraded forest, I hypothesised that forest succession is retarded in abandoned sakau plots because of a loss of advance growth after forest clearance and weeding. This would exclude advance growth from playing a major role in regeneration and prevent species relying upon advance growth from establishing in sakau plots. I compared regeneration in abandoned sakau plots with regeneration following tree-fall disturbance in intact forest. All available tree and shrub species were sampled for composition, density, height, and health. The area covered by ferns, grasses and lianas by species was scored. Light and litter were measured in the smallest sample units for analyses independent of plot types. Samples were re-measured over 15 months to track the growth and survival of the initial cohort and newly recruited seedlings.

Small single-tree falls brought only subtle changes to the forest; light varied more in gaps without necessarily producing significant shifts in mean responses. Recruitment of the pioneer canopy tree *Campnosperma brevipetiolata* Volkens and understorey tree *Aglaia ponapensis* Kaneh. was significantly greater in gaps than in mature forest. With the exception of *C. brevipetiolata*, both the initial and newly recruited mature and gap populations were dominated by heavy-seeded species. Height growth was greater in gaps.

In contrast to the forest, sakau plots were characterised by: open canopies; shallow litter depth; wide coverage of ferns, grasses and lianas; and few trees and shrubs, predominantly light-seeded small-tree and shrub species. In 15 months, seedlings and saplings grew rapidly, litter depth and fern cover increased and grass cover decreased markedly.

At a broad disturbance scale (quadrat data from all plot types combined), light was correlated with species responses such as seedling abundance and height growth; however, light was not very influential at the narrower scale of small-gap dynamics. Larger and older seedlings survived longer, but new recruits initially grew faster.

Results suggested that tree species that are better adapted for survival in Pohnpei's mature- and gap-phase forest, typically those with relatively heavy seeds, established from advance growth and/or seed rain. The prevalence of advance growth in Pohnpei's upland forest meant that mature-forest species were self-perpetuating into the gap phase. In contrast, species composition and abundance in sakau-plot regeneration reflected a greater reliance upon propagule input from the soil seed bank and seed rain. In abandoned sakau plots, the breakdown of advance growth, combined with a seed rain deficient in heavy-seeded species (Winthrop, 1998) and competition from ferns and grasses, excluded from establishment many species normally common in Pohnpei's forest, thereby impairing forest recovery. I examined the implications of this for restoration strategies.

Acknowledgements

This thesis research was part of a research programme under Dr. Nora Devoe at the School of Forestry, University of Canterbury. The programme's intention was to understand Pohnpei's upland forest dynamics in order to speed restoration of forest cover in formerly cleared and cultivated areas. This applied ecological approach aims to support and complement Pohnpei State Division of Forestry, The Nature Conservancy, and The Watershed Steering Committee in their efforts to reduce the rate of upland forest clearance on Pohnpei. These Pohnpeians are themselves working through the vital cultural and social aspects of conservation. I appreciated but did not fully understand the Pohnpeian people because, like all cultures, their culture is so rich and complex. Instead, as a *menwai* (foreigner), I brought to Pohnpei my own cultural heritage and a western ecological view of the world. I am growing an intimate and critical awareness of the way in which dominant Western society views our world. This aided my understanding of changes occurring on Pohnpei that relate to traditional Pohnpeian society converging with aspects of my own society through global economic and social Westernisation.

Throughout the process of creating this thesis, I was assisted, supported and guided by many people. Most influential of these people, and deserving my deepest gratitude, was my thesis supervisor, Dr. Nora Devoe. Her wisdom, patience, and enthusiasm helped to steer me through all the ups and downs of the PhD-creating process, balancing well the supervisor's role of professional critic, motivator, and personal supporter. However, although my supervisor helped immeasurably in shaping this thesis, the final thesis form is fully my responsibility, including any errors or deficiencies.

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As in all my life's endeavours, I was most fortunate to have received love and unwavering support from my family, plus much direct assistance from them, including computer and technical work and thesis proof-reading. I was also very fortunate to

have shared this thesis time with fellow post-graduates, particularly Didy and Krishna; friends I met on Pohnpei: Lynn, Virginia, Candace, Julie, and Cathy; as well as special friends Dellaina, Robin, Victor, and Daniel.

My final and fondest gratitude is to Pohnpei's upland forests and the human and non-human beings who are a part of and/or share its beauty, peace, resources, and abundant expression of life.

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Introduction

Chapter One: Deforestation on Pohnpei

Tropical hill or upland rainforests are diminishing rapidly[1]. Although previously less affected because of their greater remoteness and more difficult terrain than lowland forests, the rate of upland rainforest loss now exceeds that of any other tropical forest type (FAO 1993). This is mainly due to conversion to agriculture.

A prime example of current pressures on tropical upland rainforest is Pohnpei, Federated States of Micronesia (FSM), in the Western Pacific (6° 54' N and 158° 14' E, Figure 1.1). Pohnpei is a 335 km^2, volcanic, highly mountainous island[2] (Figure 1.2), inhabited by approximately 32,000 people (Pohnpei Office of the Governor 1996).

As on all small Pacific islands after sometimes-considerable initial impacts, isolation in the past compelled Pohnpeians to be self-sufficient and maintain resource integrity for survival. Following their arrival on the island at least 2500 years ago, humans gradually developed a complex agricultural system of permanent, multi-canopy tree gardens to provide food to eat, sell, and for cultural purposes (Haun 1984; Raynor & Fownes 1991). Pohnpeian tree gardens were species-diverse and held a high diversity of cultivars of important food crops such as breadfruit (*Artocarpus altilis* (S. Parkinson) Fosberg), plaintain (*Musa* spp.), and yams (*Dioscorea* spp.) (Raynor & Fownes 1991). As Pohnpeian settlements and their associated agricultural crops expanded, they completely replaced lowland forest. The settled areas, called *nansapw* in Pohnpeian which means "lands where humans settle, reside, and cultivate" (Merlin et al. 1992, p.6), were ideologically under the trusteeship of the local paramount chief (Dahl & Raynor 1996), called the *Nanmwarki* in Pohnpeian.

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[1] 'Upland forest' is the most commonly used term to describe these forests in Micronesia (DeBell & Whitesell 1993). MacLean et al. (1988, p.7) defined upland forests as "forests where palms do not predominate and where the water table is too low to support mangrove or swamp forest species". Trustrum (1996) referred to Pohnpeian upland forests as forests occurring higher than 200 m elevation, but within the uplands were upland (broadleaf) forest, palm forest, dwarf forest, and upland-palm complexes, similar to MacLean et al. (1986). For deforestation figures, FAO's (1993) upland formation comprised 'hill and montane forest'. However, upland rain forest occurs at much lower altitudes on small islands than in continental forests at similar latitudes. See Chapter 3.5 for further discussion.

[2] Approximately 60 % of the island is mountainous, with 11 peaks over 600 m elevation (the tallest peak is ~790 m); ~20 % is rolling hills and plateaus (MacLean et al. 1986). The island is ~five million years old (Keating et al. 1984).

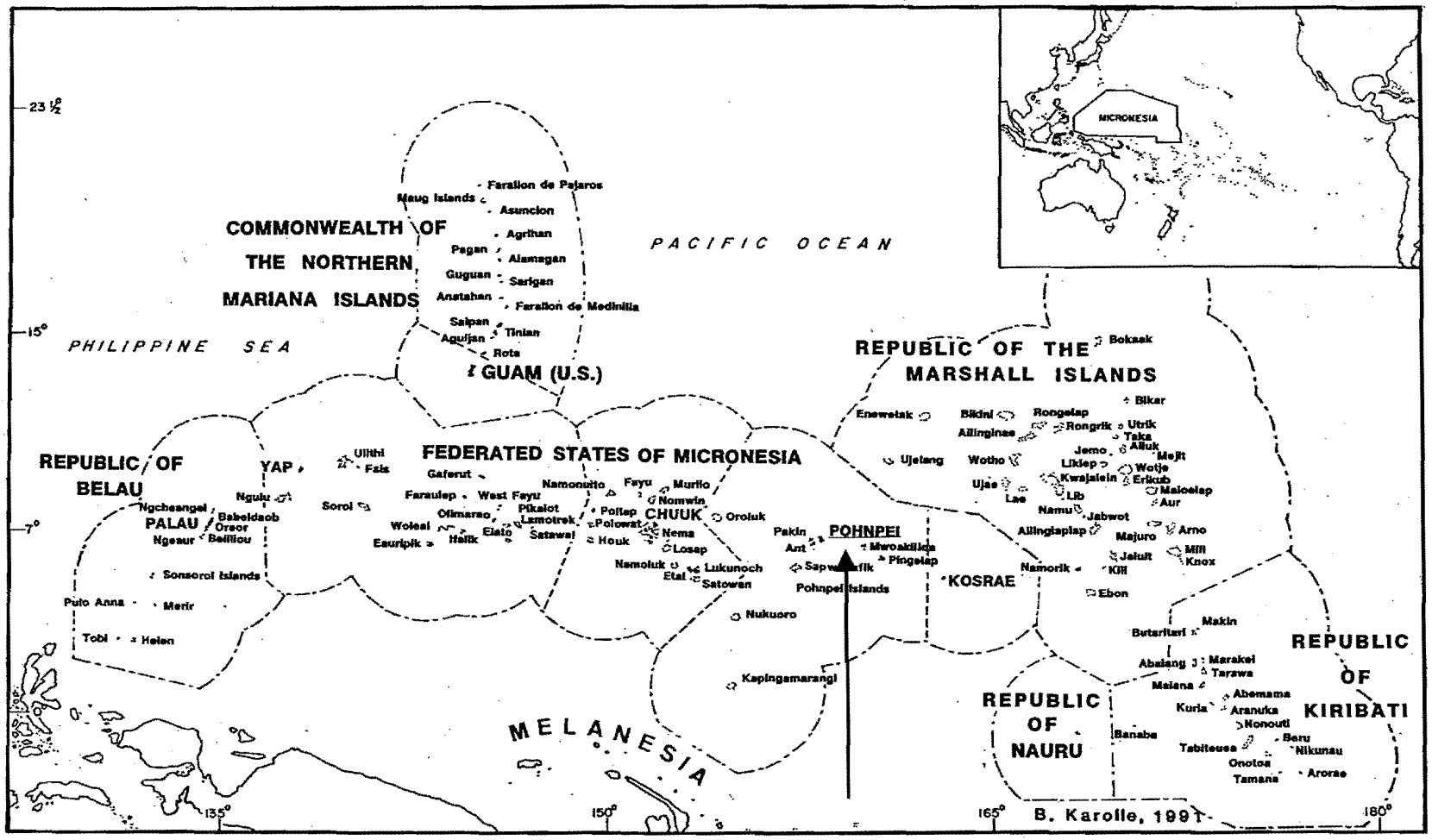

Figure 1.1 Location of Pohnpei, Federated States of Micronesia, in the Western Pacific.
Sourced with permission from Karolle (1993, p.3) (original title removed, and arrow added for emphasis)

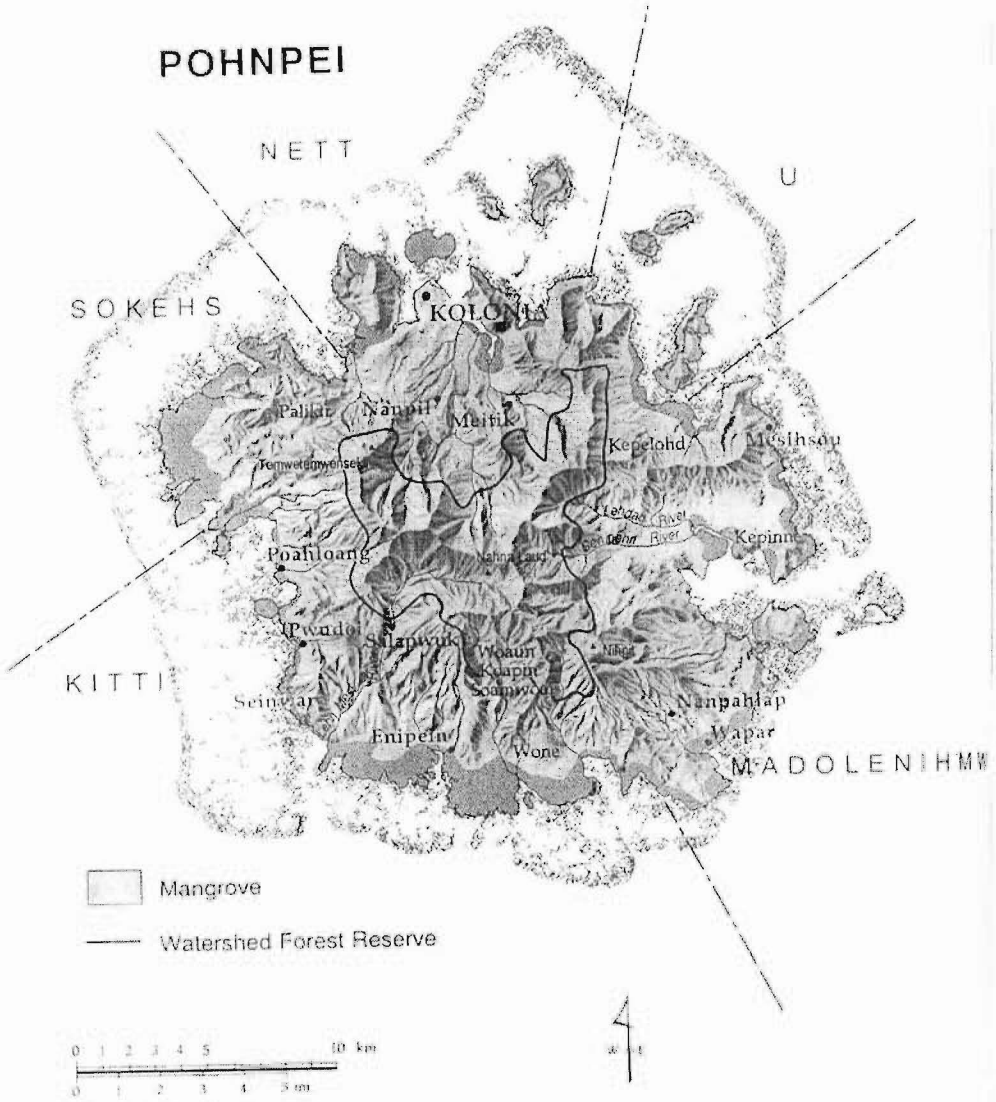

Figure 1.2 Pohnpei
Sourced with permission from Raynor (1994, p.60).

In contrast to the lowlands, people extracted limited amounts of food, timber, medicines and other products from the upland forest, but traditionally they were not encroached upon by cultivation to the same extent as the lowlands. The steep, often rocky slopes, extremely high rainfall, and greater remoteness of the upland forests made them less physically suitable for cultivation. Upland forests were politically common property, outside the official control of the *Nanmwarki*. The Pohnpeian word for upland forests, *nanwel*, meaning "wild forest lands or lands outside of human authority" (Merlin et al. 1992, p.6) conveys the reality that physically and socially, the

upland forests were largely outside of human influence. Legends often associated the upland forests in the island's central interior with evil or antisocial behaviour (Petersen, 1995). Inappropriate activity in and use of the forest showed disrespect for the spirits who were thought to dwell in and control these areas and was believed to be punishable by severe illness or death (Dahl & Raynor 1996)[3]. It was this deep-seated cultural and spiritual respect for the upland forests, interrelated with the forests' physical location and character, that helped afford their preservation. Thus, many aspects of traditional Pohnpeian culture and resource management reflected the nature of Pohnpei's physical landscape and Pohnpeians' intimate relationship with it (Petersen 1995).

Upland forests on Pohnpei are crucial to the maintenance of water quality and quantity, soil conservation, and hydro-power generation. The vegetation, litter layer and root system of the forest capture the extremely high amounts of annual rainfall,[4] retarding surface water run-off, and hence protecting against soil erosion and sedimentation of rivers and coastal waters (Raynor 1994). The slow filtering and release of groundwater stabilises stream flow, reducing both flood and drought severities (ibid.). These ecological services support Pohnpei's subsistence and cash economies in the highly populated lowland areas. Similarly, fisheries and tourism rely on high coastal water quality (White 1994).

FSM has been an independent nation, albeit an alliance of four diverse states of Micronesian islands, since 1984, but it has strong associations with the United States, the dominant power in Micronesia since the end of World War II. Pohnpei has seen a series of imperial powers laying claim to the islands since the late 1800s[5] - Spain (1886-1899), Germany (1899-1914), Japan (1914-1945), and then finally United States. Yet, Pohnpeians have always held a very strong sense of identity and showed great adaptability and confidence when dealing with *menwai* (foreigners).

Nevertheless, increasing foreign influence, particularly since the end of World War II, has brought significant change to Pohnpei, and all of Micronesia. Heavy depopulation from introduced European diseases in the late Nineteenth Century and the

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[3] This applied likewise to marine environments, which were also common property (Dahl & Raynor 1996).

[4] Mean annual rainfall is 4820 mm at sea level (MacLean et al. 1986), but is considerably higher in the mountainous interior of the island (Spengler 1990).

[5] For indepth coverage of Pohnpei's history - pre- and post-colonial, see, for example, Ashby (1993) or Hanlon (1988).

first institution of a western government structure by the Germans in 1899 initiated a period of weakening traditional culture, authority, and land tenure (Dahl & Raynor 1996). Rapid population growth in the last fifty years, combined with a change to a cash economy, propelled by short-term US aid money[6], has further weakened cultural and therefore resource management traditions (Mason 1979; Dahl & Raynor 1996; Thomas 1996; Trustrum 1996).

As a result, upland forest area on Pohnpei, including upland broadleaf, palm, and dwarf forest types, has shrunk from 42 % to 15 % of total land area over the last two decades (Trustrum 1996), largely through conversion to *sakau* (*Piper methysticum* G. Forst.) cultivation. The roots of sakau, more commonly known as *kava* (Samoan), are used to create a mildly psychoactive drug that is of great cultural importance to Pohnpeians as a way of communicating with the non-human or spirit world. Sakau was traditionally cultivated in limited lowland areas and drunk only by socially high-ranking people, but the introduction of a cash economy and the relaxation of rules to allow the general consumption of sakau after World War II has led to its commercialisation (Dahl & Raynor 1996). Sakau has become an important cash crop, especially since there are few other opportunities to earn money outside government employment. In some rural communities, cultivation and marketing of sakau is the biggest source of cash income (Raynor 1996), although the majority of the rural village population still practise a largely subsistence lifestyle. Other factors affecting forest loss include home settlements further up into the upland forest, road construction, hunting, and potentially unchecked tourism (Raynor 1994).

This upland forest loss will impact strongly on Pohnpei, particularly on the viability of the upland forest ecosystem and its inhabitants. Several of Pohnpei's rare bird species, for example the short-eared owl (*Asio flammeus*) and the long-billed white-eye (*Rukia longirostris*) will be under serious threat of extinction in the next decade unless forest clearing is controlled (Thomas 1996). Endemic species on islands, for example the long-billed white eye, are at great risk because there are no other sources for new individuals beyond that island. As birds become more threatened, plant species relying upon birds for seed dispersal will be at increasing risk, with rare species at greatest risk (Diamond 1975; Craig 1993; Elmqvist et al. 1994).

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[6] Strictly speaking, the Compact of Free Association with USA up to 2001 is rent, rather than discretionary aid, paid for exclusive US access to FSM's waterways for military use (Osman 1995, p.6). Under the Compact, however, FSM is also eligible for additional US government agency grants (ibid.).

Upland forests on islands are also susceptible to invasion by exotic species after disturbance (Palmer 1988; Walker & Vitousek 1991; Elmqvist et al. 1994; Bellingham et al. 1995; Medeiros et al. 1995).

Despite their small size, the range of elevations, areas and topographies of mountainous Pacific islands offer a wide range of habitats (Holdgate & Nicholson 1967), especially for endemic and rare flora (Straatmans 1964). On Pohnpei, over 550 vascular plant species have been described (Glassman 1952), with endemism at 14 %. The upland forest is habitat for at least 269 of these plant species, 110 of which are endemic, 90 % of all Pohnpei's remaining endemic plant species (Raynor 1994). Twenty-five of the island's 33 resident bird species use the upland forest extensively (Thomas 1996). Five bird species are endemic (Engbring et al. 1990; Buden 2000). However, numbers of Pohnpei's forest bird species decreased between 1983 and 1994, many quite dramatically (Buden 2000), probably as a result of the large habitat loss. Thus, the loss of upland forest habitat will reduce indigenous bio-diversity. Furthermore, as Pohnpeian culture is so interwoven with its physical landscape, the loss of upland forest and its inhabitants reflects a loss of social self.

With forest loss, the provision of important water and soil functions and forest products that humans rely upon downstream may be impaired. Lower evapo-transpiration rates from forest loss generally result in increased mean stream flow, flood peaks and drought lows (Reid 1993; Vertessy 1999), with the on-stream flow amplified in high rainfall areas such as in Pohnpei's uplands. Removing vegetation on the steep upland slopes may also pre-dispose the slopes to landslides (Trustrum 1996). Siltation caused by increased water runoff and soil erosion may threaten lagoon and reef ecosystems, in turn threatening the resource base for tourism and fisheries. However, erosion from unpaved roads rather than sakau cultivation is presently the main cause of sedimentation in Pohnpei's rivers (White 1994).

United States funding to the Federated States under the 1985 Compact of Free Association ceases in 2001. Although the Compact is to be renewed, funding may be considerably lower than it has been over the past 15 years. At present up to 80 % of total Pohnpei State Government revenue comes from US aid/rent (FSM Office of Planning and Statistics 1991), with the government spending much of this in salaries and wages as the largest, and generally highest paying, employer. Food supplies, mostly rice, flour, and processed meats, are increasingly imported because for wage earners who buy their food, imported items like rice, flour, and canned fish are cheaper

and perhaps more prestigious than the local foods, even though they are generally of poor nutritional quality (Schoeffel 1992). However, imports far exceed exports (MFAT 1994), and reliance on imported foods only reinforces Pohnpeians' dependency on international aid and a global economy over which they have no control (Mason 1979; Schoeffel 1992). The limited land area of small Pacific islands necessitates sustainable, multiple use of resources. Western-style large-scale, single-crop agriculture is particularly inappropriate to islands (Dahl 1985), but as US funding to the FSM government declines, cultivation for sakau and other cash crops will probably increase. The pressures placed on Pohnpei's natural resources will be exacerbated as people search for cash-generating alternatives to government wages to maintain their material expectations.

A Pohnpeian community-based management initiative is addressing the island's rapid deforestation. The Watershed Steering Committee, which formed in 1990, aims to reduce the rate of conversion to sakau by promoting strong community participation in decision-making related to the forests (Raynor 1995; Dahl & Raynor 1996; Tilling 1997). A "grow lowland" campaign is currently mass-planting sakau at low elevations to dissuade growers from planting in the uplands. Environmental matters are now one of the six negotiating sectors for US-FSM Compact renewal talks, along with education, health, governance/capacity building, private sector, and infrastructure.

Nevertheless, large areas of degraded forest exist and present deforestation rates across the island are still very high. These disturbed areas need to be restored to recover ecological functioning of the upland forest ecosystem. In order to promote and accelerate restoration of degraded areas, it is necessary to know the ecology of the undisturbed forest and how the forest naturally regenerates as a point of comparison with regeneration following cultivation. The importance of such ecological research was emphasised by DeBell and Whitesell (1993, p.7) in their discussion of the future of Micronesia's upland forests:

> *Knowledge of the basic silvics of forest trees and stands is the biological foundation for management and utilization of productive forests, for restoration and preservation of endangered trees and stands, and for the reclamation of degraded sites.*

Allum (1996) found sakau-disturbed forest sites differed significantly in species composition and density from mature-phase forest. Regeneration was retarded on

cultivated sites with retardation being exacerbated the longer a site was cropped and the larger the site cleared. However, the mechanisms operating to produce these different compositions were unknown.

Research aim

The aim of this research then was to understand forest regeneration processes under natural and anthropogenic conditions by studying a mechanism of regeneration known as advance growth. Knowledge gained from this research and that of Allum (1996), Gardner (1997), and Winthrop (1998) will provide the basis for the design of management interventions to speed forest restoration in areas cleared for sakau cultivation.

Advance growth is an important regeneration mechanism for late-successional species (Uhl et al. 1988). Seeds germinate and establish in the shaded understorey of a mature forest canopy and grow slowly until conditions favour more active growth. A disturbance event, often a tree-fall, creates an opening that alters the micro-environment within and around the gap. Pre-existing individuals that survive tree-fall gap creation are able to accelerate their growth and successfully compete for new resources, particularly increased light. Advance growth, seed rain (seeds dispersed into gaps from surrounding adult trees), germination of seeds held dormant in a soil seed bank, and re-sprouting of larger trees together form the mechanisms by which species re-establish a site.

Sakau cultivation involves almost complete clearance of the canopy and understorey surrounding sakau plants, eliminating advance growth. This loss of the main regeneration mechanism for late-successional species could account for the altered composition of the regeneration between mature forest and cultivated agro-forest documented by Allum (1996), and could represent the greatest barrier to forest succession on formerly cultivated sites. It was therefore vital to address questions concerning the role of advance growth in the regeneration processes of these forests and the ways by which disturbance affects advance growth.

Except for the lowland rainforest on Kolombangara island, Solomon Islands (Whitmore 1974, 1989), rainforest ecology in the small islands of the Western Pacific has been little studied. On Pohnpei, Sheely's (Sheely et al. 1993; Sheely 1995) work

on *Campnosperma brevipetiolata* Volkens, and the University of Canterbury research project under Dr. N. Devoe (Allum 1996; Gardner 1997; Winthrop 1998), of which this thesis is a part, have been the main ecological studies in Pohnpei's upland forests. Most other research has been floral and descriptive only (e.g., Glassman 1952; Hosokawa 1967; Fosberg & Sachet 1975; MacLean et al. 1986).

The specific objectives of this thesis and the hypotheses they address are stated in Chapter 3.1 after first reviewing relevant aspects of the scientific theory pertaining to forest regeneration (Chapter Two).

Chapter Two: Theoretical Perspectives

2.1 Gap-Phase Regeneration and Forest Dynamics

2.1.1 Introduction: the gap-phase in a forest life cycle

The current scientific paradigm for regeneration of forests is the gap-phase regeneration theory. Gap-phase regeneration emphasises disturbance as the major regenerative force for most species. Disturbance plays an essential role not only in forests but also in most natural ecosystems (see Pickett & White 1985).

Plant regeneration in a forest mostly follows disturbances rather than occurring continuously. The creation of gaps in a forest canopy, ranging from single tree-falls to widespread, cyclonic blow-downs, alters the micro-environment on the forest floor, especially light levels. This provides a cue for selected seeds and seedlings to grow actively in the absence of a developed (and therefore strongly competing) forest overstorey. The spatial and temporal heterogeneity of disturbance events results in a range of micro-environmental conditions. How plant species respond to the vacated growing space and new micro-environmental conditions, and the way in which they interact with other organisms (inter- and intra-specific plant competition, seed dispersal and predation, herbivory, pathogens, mutualism) determine which plants are likely to grow in a particular gap. At any time, the floristic composition and relative abundance of species in the forest will reflect the changing hierarchy of plants as they respond to their dynamic abiotic and biotic environments.

Gap-phase processes apply to both temperate (e.g., Jones 1945; Watt 1947; Oliver 1981; Runkle 1985; Veblen 1985; Barden 1989; Spies & Franklin 1989) and tropical forests. The specific role and importance of gap-phase regeneration in tropical forests was explicitly defined in independent discussions by Oldeman (1978), Hartshorn (1978; 1980), and Whitmore (1975; 1978). However, several earlier researchers had already noted disturbance as sites for regeneration in tropical forests (Kramer 1933; Aubreville 1938; Richards 1952; van Steenis 1958). Aubreville was among the first ecologists to suggest that rainforest communities may not be stable and

static (also see Kramer 1933). Rather than a forest succeeding to a climax then remaining static in its floral composition, Aubreville thought mature (climax) forest was dynamic. Species composition varied spatially and temporally as the dominant canopy species in a particular area became replaced by other species. Richards (1952, p.49) interpreted this as the cyclic or mosaic theory of regeneration: the species composition of a small area of tropical rainforest varies in space and time and no combination of species is in permanent equilibrium with the environment. Over a large area, climate, topography and soil factors determine the general forest pattern (Webb et al. 1972) so the forest may appear stable. However, within the area is a mosaic of small patches (as coined for temperate ecosystems by Watt 1947), each patch dynamically related to others (Webb et al. 1972).

The life cycle of a tropical rainforest can be conceptualised as having different growth phases. A commonly used model consists of gap, building, and mature phases (Watt 1947; Whitmore 1975)[7]. Creation of a canopy opening promotes re-establishment of the disturbed site by germinating seeds or existing seedlings and saplings that survived the disturbance (gap-phase). Individual seedlings and saplings grow and compete strongly for resources (the building phase). The surviving matrix of individuals then eventually matures, with an associated redevelopment and maintenance of a mature, closed-canopy forest (mature phase) until a new disturbance occurs (Whitmore 1975). A forest is comprised of a mosaic of patches at these different stages of growth and maturity. Gaps are thus integral and vital components of the overall forest-growth cycle. Whitmore (1975) considered the gap phase to be the start of the cycle since the size of the gap determines the size of the forest patch.

Oldeman (1978) and Oliver (1981) presented similar life-cycle models. Oliver's model, derived from North American forests, perhaps most explicitly includes the role of advance growth in the forest life cycle. In the first of four phases, stand initiation is where pre-existing seedlings and saplings on the forest floor plus newly germinated seeds, invade the released light and soil growing space made available by a gap. As growing space is occupied and a competitive plant hierarchy among the new generation develops, some of the new generation are reduced (stem exclusion phase). A new cohort of advance growth then establishes in the understorey as the overstorey

[7] Watt (1947) also included a breaking-down phase after maturity.

matures (understorey reinitiation phase), and finally, in the old growth phase, the overstorey gradually dies and seedlings and saplings fill their places.

2.1.2 Development of gap-phase theory: factors affecting plant composition and dynamics in gaps

In the last two decades, research into the mechanisms of tropical rainforest regeneration in the gap phase has proliferated. Research has concerned all factors occurring within, influencing, and/or interacting with the gap phase. The following discussion concentrates on factors that most directly affect the composition and dynamics of plant species in forest regeneration since it is plants, particularly advance growth vegetation, that were studied in the present thesis. The factors considered most to affect plant composition and dynamics in a gap are the forest disturbance regime, the resulting gap micro-environmental conditions, species responses to these micro-environmental conditions, biotic interactions among organisms in a gap, and chance.

Disturbance regime: the gap event and its characteristics

Gaps are unique environments, varying in size, shape, and orientation based upon the disturbance events that produced them. The type of disturbance in a forest depends upon factors operating at several scales. At a forest-wide scale, forest location (latitude, longitude, and altitude) determines the climate (especially rainfall) and extreme weather events, for example, the cyclone belt 10-20° either side of the equator, fire in dry areas, or proximity to volcanoes, fault-lines, etc. On a smaller scale, soil and topographic factors can predispose forests to tree-fall disturbance. Knowledge of the disturbance history of a site aids interpretation of forest composition and structure because the current flora reflects previous disturbances (Johns 1986; Whitmore 1989).

Gap sizes range from branch-falls from gradually disintegrating trees or from fallen liana tangles, through single- and few-tree, wind-driven tree-falls, to gaps several square kilometres in area produced by cataclysmic floods, volcanoes, fire, earthquakes, or cyclones (Whitmore 1974, 1975; Brokaw 1985b). Disturbances can also be diffuse, for example, gradual leaf defoliation in a group of trees. Most gaps in tropical forests that have been studied are small (less than about 150 m^2) and caused by falling branches or trees (one or a few) (Hartshorn 1978; Sanford Jr. et al. 1986; Uhl et al. 1988; Brokaw 1996; Green 1996). Yet, although rarer in occurrence, a considerable

portion of the total area covered by gaps is attributable to relatively few, large, multiple tree-falls (Sanford Jr. et al. 1986). For example, on Christmas Island in the Indian Ocean, an island not subject to frequent, large-scale disturbances, gaps range in size from 17 to 700 m^2 but 90 % of all gaps are 120 m^2 or smaller (Green 1996). Pohnpei lies outside the main cyclone belt, but cyclones do occasionally hit the island.

Tree-falls are usually caused by wind and are most likely to occur when the soil is highly saturated due to the loosening of root holds and rain weighing down limbs and foliage (Whitmore 1975; Brokaw 1985b, 1996). Gaps can enlarge over time where trees growing on gap edges are more susceptible to wind damage (Whitmore 1975; Putz & Milton 1996). This is possibly due to turbulence in the gap or a weakening of neighbouring tree root systems by the original tree fall (Hartshorn 1980). Gaps in some forests are spatially clustered (e.g., Poorter et al. 1994; Yavitt et al. 1995; van der Meer & Bongers 1996b). This may be due to an increased susceptibility of neighbouring trees, local wind gusts that result in the simultaneous fall of several nearby trees, and/or soil and topographic patterns that influence forest structure and tree rooting thereby predisposing certain areas to more disturbance (Poorter et al. 1994). Van de Meer and Bongers (1996b) found no evidence for increasing susceptibility of neighbouring trees in their clustered gaps, and thought clustering was related most to soil factors (van der Meer & Bongers 1996a). In seasonal forests, the creation of tree-fall gaps usually peaks in the rainy season (Sarukhán 1978; Brokaw 1996).

Individual trees can fall either by the trunk snapping, particularly under rain-load, or by the whole tree uprooting. Trees can also remain "standing dead", as senescent trees gradually disintegrate. These tree-fall types produce different gap sizes and characteristics. Gaps from standing-dead trees and any associated branches are generally very small because the main trunk of the tree can remain upright for a considerable time, falling in pieces. Uprooted trees usually produce larger gaps than snapped ones (Putz 1983; van der Meer & Bongers 1996a) because they pull up a root plate in addition to other damage and the trees themselves tend to be taller and wider than snapped trees (Putz 1983; Walker 1991; but c.f. Bellingham 1991; Bellingham et al. 1992). Physical factors such as wind, rain, soil and topography (Brokaw 1985b), as well as wood properties (Putz 1983; Arriaga 1988) determine whether a tree snaps or uproots.

The most commonly used gap definition is an opening in the forest extending down through all foliage levels to an average height of two metres above the ground (Brokaw 1982). Brokaw's definition has been criticised for being ecologically inadequate (Brandani et al. 1988, Popma et al. 1988, Lieberman et al. 1989, Smith et al. 1992, Brown and Whitmore 1992, Green 1993, Lieberman et al. 1995). It may underestimate gap areas by a considerable margin (Popma et al. 1988, Green 1993). Despite this, few alternative definitions have been offered, primarily due to the inherent problem faced in trying to define discrete gap boundaries when in reality the gap edge intergrades with closed canopy forest.

Gap micro-environment

The creation of a gap alters the micro-environment within and around the disturbed area. The gap causes changes in microclimate (light, humidity, air and soil temperature, soil moisture), and possibly litter depth, root competition, nutrient release, and mycorrhizal infection.

Light is an important factors affecting plant responses in a gap. Light levels in the shaded understorey of a rainforest are characteristically very low - 0.5-5 % of the photosynthetically active radiation (PAR - light within the wavelengths 400-700 nm) (Chazdon & Fetcher 1984a; Canham et al. 1990; Smith et al. 1992; Rich et al. 1993; Whitmore et al. 1993). This depends upon the height of the canopy (Chazdon & Fetcher 1984a), as well as architectural differences among dominant canopy species and the amount of understorey and subcanopy vegetation (Kabakoff & Chazdon 1996). Light can reach the forest understorey as direct-beam light, penetrating down through a canopy opening when it is in line with the sun, or as diffuse (or indirect) light, which enters a canopy scattered off the atmosphere (Rich 1989). The closed canopy understorey has a high far-red to red wavelength ratio of light because plant foliage and litter absorbs mostly red light as the light filters vertically through the canopy (Bazzaz 1991). Sunflecks, shafts of direct sunlight that penetrate small openings in the canopy (Chazdon 1988), contribute to the total light available in closed canopy understoreys (Evans 1939; Ashton 1958; Pearcy 1983; Chazdon & Fetcher 1984a; Chazdon 1988). For example, in a Hawaiian forest, sunflecks contributed approximately 40 % of all light reaching the understorey (Pearcy 1983). The length of time that sunflecks are present per day is highly variable and depends upon cloudiness and canopy structure (Pearcy 1983); it increases steeply from the subcanopy (Ashton

1958). Light can vary spatially by a factor greater than two in closed-canopy understoreys within two metres, largely due to the effect of sunflecks (Chazdon & Fetcher 1984b).

When a tree falls, PAR penetrating to the forest floor increases. Post-gap light is spectrally very different from that normally found under a closed canopy (Lee 1987). Gap creation increases the level of red light reaching the forest floor, with important consequences for seed germination in some species (Bazzaz 1991). The duration, intensity and spectral distribution of light received in the gap understorey depends upon the gap's size, shape, orientation, slope and aspect; the sun's position, weather variables such as cloudiness and humidity, height of the surrounding closed canopy forest, the vertical stratification of the forest, and the characteristics of post-tree-fall debris and surviving vegetation (Denslow 1980; Chazdon & Fetcher 1984b; Brokaw 1985b; Devoe 1992). Seasonal variation in light reaching closed forest understoreys and gaps has been noted (Chazdon & Fetcher 1984a; Lee 1989; Raich 1989). Gap edges and small gaps (<100 m^2) generally have higher levels of diffuse light and more sunflecks than closed canopy forest (Chazdon & Fetcher 1984a). Differences in light between gaps and closed canopy forest tend to increase with increasing gap size, and are greater at gap centres rather than gap edges, and on sunny over cloudy days (Denslow 1987). Light at the gap centre relates to the size of a canopy opening (Brown 1993; Denslow et al. 1998). Beyond that, however, the very high spatial heterogeneity in light within individual gaps and indeed within mature forest precludes dichotomous characterisations between gap and non-gap light environments or between differently sized gaps (Denslow & Gomez Diaz 1990; Devoe 1992; Smith et al. 1992). For example, light can penetrate through canopy openings in Malaysian dipterocarp forest to at least 20 m inside the forest from the nearest gap (Raich 1989).

Changes in air and soil temperature and relative humidity are evident with increasing light penetration to the forest floor. Values for these variables are higher and fluctuate more at gap centres than under closed canopy forest (Vitousek & Denslow 1986; Longman & Jenik 1987; Luizao et al. 1998); extremes in air temperature increase with gap size (Luizao et al. 1998). The presence of litter, which is locally highly variable, can modify local soil-surface temperature (Molofsky & Augspurger 1992).

With the decay of tree-fall debris, short-term nutrient fluxes might be expected within gaps. However, neither Vitousek and Denslow (1986), Uhl et al. (1988), nor

Luizao et al. (1998) could detect any significant differences in nutrient availability between gaps and closed forest. Gaps can actually reduce nitrogen availability initially (or for long periods after large disturbances) because it is tied up in the microbial biomass decomposing the woody debris (Zimmerman et al. 1995). Vitousek and Denslow (1986) observed that nitrogen and phosphorus availability were dramatically reduced in the root-pit zone because of the surface deposition of nutrient-poor subsoil. Luizao et al. (1998) found no significant differences between mid-sized gaps (~150 m^2) and closed forest for microbial biomass, soil respiration, or nitrogen mineralisation, only observing nutrient release from decomposition in the crown zone.

Orians (1982) and Oldeman (1978) predicted that light and nutrients would differ among gap microsites associated with the root, bole, and crown zones of a tree-fall, resulting in different species compositions. When tested by Brandani et al. (1988), microsite zones were more similar to zones of the same type among gaps than they were to different zones within the same gap. Yet Uhl et al. (1988) found that woody plant density in multiple tree-fall gaps appeared to be unaffected by microsite type except in the root-pit zone due to the loss of advance growth. Pioneer species may be concentrated on the mineral soil of the root-pit zone (Putz 1983).

A temporary decrease in below-ground competition with the fall of established trees has been suggested (Richards 1952; Whitmore 1975; Hartshorn 1978; Brokaw 1985a; Grubb 1996). Live root biomass is diminished within gaps compared to closed-canopy forest (Silver & Vogt 1993; Wilczynski & Pickett 1993; Ostertag 1998), especially after very large and/or multiple disturbances (Silver & Vogt 1993). However, the extent to which the reduced root biomass affects root proliferation and tree growth in gaps is unclear and may depend upon soil types (Ostertag 1998). Coomes and Grubb (1998) found that below-ground competition affected juvenile plant growth but impacts were of similar magnitude in gaps and closed canopy forest. Allen et al. (1998) did not find significantly different mycorrhizal infection in gaps compared with closed forest.

Thus, the micro-environment within gap-phase forest is highly variable, but generally PAR within gaps is significantly greater than under a closed canopy, particularly in the red light spectrum. Small gaps and large-gap edges tend to have higher levels of diffuse light and more sunflecks than closed-canopy forest. Air and soil temperatures have greater extremes within gaps, and relative humidity is lower. Gaps also have more variable litter cover, and may experience less root competition.

Plant regeneration strategies: species responses to the gap micro-environment

Combinations of characteristics or strategies related to establishment, survival and growth under different conditions vary among species. These strategies influence how species respond to changes in the understorey micro-environment following a disturbance. Grime (1979, p.1) defined a strategy as a group of similar or genetic characteristics that recur widely among species or populations and cause them to exhibit similarities in ecology. Whitmore (1975) defined two tree species regeneration strategies (renamed "character syndromes" in Whitmore (1978)) based upon the differential establishment and survival success of each species in differently sized gaps. He ascribed to each group the following characteristics:

- *Light-demanding or pioneer species*: seeds germinate in a gap from seed rain (recent arrivals from surrounding seed trees) or from dormant seeds in the soil seed bank; have rapid height growth in youth with low density wood, flower and fruit copiously and frequently, and disperse efficiently and widely; species can be short or long-lived.
- *shade-bearing or shade-tolerant species*: seeds germinate in the shade of the closed forest, mostly from continuous seed rain rather than a seed bank; slow growing with dense wood; existing seedlings and saplings respond to the changed environment, most often succeeding in small gaps rather than large; can regenerate and persist, often for several years, in the shade of the high forest; large, animal-dispersed propagules.

These strategies or characteristics are referred to commonly in published research by the above names, or variants including pioneer versus primary species (Brokaw 1985b; Brokaw 1985a), large gap specialists versus small gap specialists (Denslow 1980), and early and late-successional species as used most often in this thesis (see Swaine & Whitmore 1988, p.83, for other terms). Most plants in tropical rainforests are from species classified as climax/shade tolerant. Whitmore (1975) stated that these two strategy profiles are extremes; species form a continuum between the strategies. For example, Whitmore also presented four strategy classes based upon the forests in Solomon Islands (1974):

1: species that germinate, establish, and grow in closed forest.

2: germinate in closed forest but survive and grow in closed forest or gaps.

3: can germinate in gaps or closed forest but need gaps to survive and grow.

4: mostly germinate in gaps and can only grow and survive in gaps.

Denslow (1980) hypothesised that interspecies competition is highly important in determining the relative abundance of species in gaps and closed forest. Gap-size partitioning (or niche differentiation) assumes that species are preferentially and specifically adapted to compete successfully in a particular regeneration niche along the gap size continuum. This necessarily means that they have made adaptive compromises in their regeneration strategies and are not able to compete well in other areas of the temporal and spatial gap environment. However, evidence for gap-size partitioning is inconclusive or negative (Barton 1984; Brokaw 1985a; Hubbell & Foster 1986; Brokaw 1987; Lieberman et al. 1989; Welden et al. 1991; Brown & Whitmore 1992; Clark & Clark 1992; Kennedy & Swaine 1992; Oberbauer et al. 1993; Lieberman et al. 1995; Brown & Jennings 1998; Thompson et al. 1998). For example, Barton (1984) found only weak evidence for climax species preferring small gaps and edges of large gaps, and pioneers preferring large gap centres. The combined density of the six shade-tolerant species that he studied was not significantly different between small and large gaps. Barton found much overlap among early and late-successional species among gap sizes. Brokaw (1985a) found that in general, pioneers only colonise large gaps but climax species can regenerate in both large and small gaps when disturbance intensity is not too severe. Even among the small subset of pioneers that Brokaw studied, species formed a gradient in terms of recruitment, growth and light requirements, and occupied completely overlapped niche distributions (also see Brokaw 1987). Nevertheless, species may partition the micro-environmental gradient within gaps and mature forest, especially light (Devoe 1992; Svenning 2000), depending upon the species and the scale of observation.

Thus, there is no clear relationship between gap size and germination, establishment, growth and survival of pioneer and climax species (Welden et al. 1991; Brown & Whitmore 1992; Clark & Clark 1992; Devoe 1992; Kennedy & Swaine 1992). Within-gap heterogeneity is regularly as great as or greater than between-gaps (Kennedy & Swaine 1992). For example, the edge area of a large gap may provide a greater number of potential sites for a climax species than a small gap itself (Brown 1993). Also, the presence of advance growth means that regeneration in gaps is often

dominated by the tallest advance growth at the time of gap creation (Brown & Whitmore 1992; Midgley et al. 1995; Brown & Jennings 1998) rather than by a species that is specifically adapted to that micro-environment. Hubbell et al. (1999) concluded that gaps are important for species diversity but mainly by being sites of increased seedling and sapling densities rather than each species having niche preferences for specific gap sizes.

Species responses to gaps may vary with life-history stage. For example, Svenning (2000) found that some understorey plant species occurred preferentially in higher-light areas at all life history stages, whereas other species occurred in higher light when small but were indifferent as established and larger plants; or vice-versa. Others again occurred regardless of life history stage or light. Clark and Clark (1992) also found size-dependent patterns among species. For some large-seeded, late-successional species, early establishment is best in more shaded sites, but once established, height growth improves with increased light (Devoe 1992). In Panama, sapling survival is generally lower or indifferent in higher-light forest areas than in more shaded areas, whilst sapling growth is faster or not significantly different in higher light than in more shaded areas (Welden et al. 1991).

Gap recruitment and establishment mechanisms

The main basis for Whitmore's (1975) regeneration character dichotomy was a distinction in the type of establishment mechanism(s) used by each species. A species can establish in a gap through germination of seed either dispersing into a gap at the time of or after gap creation (seed rain) or held dormant in the soil seed bank of the site, from growth of pre-established seedlings and saplings (advanced growth), and/or vegetative re-establishment through sprouting from damaged vegetation. These mechanisms are outlined below.

The intensity and nature of the disturbance producing the gap determines the relative importance of the main establishment mechanisms to regenerating species composition and relative abundance (Bazzaz 1984; Connell 1989). A large disturbance such as a landslide may remove all organisms, including advanced growth, and all buried seeds, so regeneration must originate from the seed rain. In contrast, a single tree-fall gap is a less intense disturbance, so a portion of the advance growth, and the

soil seed bank, survives. In this case, regeneration can originate from all sources (Bazzaz 1984, p.235; Connell 1989).

- **Seed dispersal, dormancy, and germination**

The first three mechanisms stated above are derived from propagule inputs as the result of plant sexual reproduction and rely upon many biotic interactions in order to reach a site. Most tropical rainforest species rely on animals for seed dispersal (Denslow & Gomez Diaz 1990; Terborgh 1990). Frugivore-fruiting-plant interactions in gaps may be very important in structuring tropical forest communities because a higher proportion (relative to area) of frugivores and fruiting understorey plants are found in maturing gaps than in closed forest (Levey 1988).

The probability that a fruiting tree has its seeds dispersed depends upon the dispersal agent as well as factors affecting that dispersal agent. Predation of animal fruit and seed dispersers is an important consideration in tropical rainforests (Snow & Snow 1986). Recently created gaps are probably dangerous sites for frugivorous birds and bats (Schupp et al. 1989; Devoe 1990). Howe (1979) theorised that birds will tend to feed quickly in the copiously fruiting trees in gaps then move to the relative safety of the surrounding foliage to process the fruits, dropping seeds below where they perch. Gap edges may therefore be important germination and seedling establishment sites, especially if trees surrounding a gap are susceptible to gap enlargement.

Spatial foraging and habitat preferences of seed dispersers influence the composition and relative densities of plant species growing in a tropical rainforest (Loiselle et al. 1996). In comparisons of seed rain in tree-fall gaps and closed-canopy sites in Costa Rica (Loiselle et al. 1996) and in Puerto Rico (Devoe 1990), animal-dispersed species dominated the seed rain, but fell in greater amounts in the closed forest sites. In contrast, a greater proportion of seeds arriving into tree-fall gaps was wind-dispersed than in the closed forest. These results corroborate predictions made by Schupp et al. (1989). Denslow and Gomez-Diaz (1990) also found that animal-dispersed seeds, many of them originating from over 50 m away, dominated seed rain in gaps.

Seed predation of dispersed seeds can decimate very high proportions of a seed population depending on the species, seed deposition site, time, and chance (Schupp 1988a). Schupp (1988b) found seeds and young seedlings of a subcanopy tree in tree-

fall gaps subject to disproportionately high predation by rodents, maybe because tangled vines, branches, and litter allowed rodents to hide and predate in gaps more than in closed forest. Nevertheless, even if predators remove many seeds, the remaining dispersed seeds should have greater chances of survival by having moved away from the high seed and seedling densities near the parent plant and by seed burial (Sork 1985). Due to the high temperature and soil moisture in the tropics, seeds are also highly vulnerable to pathogen and parasite attack, both pre-dispersal (Kitajima & Augspurger 1989), and post-dispersal but pre-germination (Ng 1978; Augspurger 1990).

Most seeds of rainforest species tend to germinate quickly after dispersal (Ng 1978; Vázquez-Yanes & Orozco Segovia 1993). Yet, even many rapidly germinating species maintain some sort of short dormancy period (Ng 1980; Garwood 1983; Devoe 1992). Transit through the gut of an animal may be one of the principal factors triggering seed germination among animal-dispersed seeds due to the erosion of hard seed coats, high temperature and moist conditions (Vázquez-Yanes & Orozco Segovia 1993). Yet, some studies indicate that there is little difference between responses of seeds taken directly from the fruits and those taken from the faeces of animals (Vázquez-Yanes & Orozco-Segovia 1986). Ng (1980) suggested that such endogenous dormancy in tropical rainforest seeds may be to disperse seeds by animal seed vectors as far as possible from parent trees.

Germination of some species' seeds is inhibited not by endogenous characteristics like hard seed coats but by environmental factors, especially light conditions, that prevail in the closed forest (Vázquez-Yanes & Orozco-Segovia 1990). These seeds have environmental sensors that delay germination until appropriate microclimates occur. Pioneers use this type of dormancy most commonly and are consequently the most abundant components of the soil seed bank (Whitmore 1983; Vázquez-Yanes & Orozco Segovia 1984). Environmentally controlled seed dormancy in the tropics is much less frequent among climax trees than pioneers and other woody plants (Vázquez-Yanes & Orozco Segovia 1993). Tree-fall gaps result in a greater temperature fluctuation at the soil surface because of the direct insolation, which increases light intensity (photosynthetic photon flux density, PPFD) and increases the ratio of red to far-red (R:Fr) light required for many dormant seeds to initiate germination. Seeds lying dormant in the soil seed bank respond to these changes in the micro-environment although species differ in the ratio of R:Fr required to induce

germination and in the length of time the higher R:Fr must be maintained to induce germination.

Seed germination in seasonal rainforests tends to peak soon after the beginning of the rainy season (Garwood 1983). Seedling emergence in new gaps in Panama peaks two weeks into the rainy season whereas seedling emergence in shaded understorey plots peaks six weeks later than in light gaps (Garwood 1996b). In Puerto Rican forest, Everham et al. (1996) found that high light and litter assisted germination of most species, except very small-seeded, early-successional species, yet species were unable to be grouped based on germination cues. Devoe (1992) found that heavier-seeded species dispersed and recruited more beneath closed canopy sites than in gaps. In general, recruitment of species with heavier seeds increased with decreasing light and occurrences of only 15 % of species tested were not significantly related to quadrat light levels (ibid.).

Gaps in the litter layer, though operating on a much smaller scale than canopy gaps, appear to be very important for the germination and establishment of small-seeded species (Grubb 1996). Although leaf litter can maintain high moisture levels in the soil suitable for germination of some species, often it can act as a physical barrier to establishment of small-seeded species that lack the reserves required to penetrate the litter and reach mineral soil (Vázquez-Yanes & Orozco Segovia 1993). Litter also preferentially transmits longer wavelengths of light, reducing the R:Fr ratio to a level that can inhibit germination of light-controlled dormant seeds (ibid.). Consequently, litter tends to reduce germination rates of small-seeded species, whilst large-seeded species have either similar or less germination when litter is removed than when it is retained (Guzman-Grajales & Walker 1991; Molofsky & Augspurger 1992). The degree to which species are affected by litter depends upon the life-history stage (germination vs. seedling survival rates), litter depth, and the interaction of litter and light (Molofsky & Augspurger 1992). For example, germination of some shade-tolerant species was higher under litter than on bare ground in sunny sites but there were no differences in shaded sites (ibid.).

Regeneration via the seed bank increases with increasing light (Devoe 1992). In Devoe's study, no regeneration came from the soil seed bank in low light plots except for two fern species. Lawton and Putz (1988) found the seed bank was the main source of seedlings on exposed soil in gaps in lower montane rainforest, as did Putz

and Appanah (1987) in lowland rainforest gaps. Seed banks play a dominant role in early-successional sites after forest clearance (Young et al. 1987; Devoe 1990).

- **Advance growth**

Advance growth plays an important role in regeneration of gaps, especially small ones (Richards 1952; Fox 1973; Whitmore 1975; Denslow 1987; Uhl et al. 1988). In several forest studies, seedlings that survived gap creation, that is, advance growth, and individuals establishing soon after gap creation showed significantly higher growth rates and lower mortality than those establishing later (Brokaw 1985a; Brokaw 1987; Uhl et al. 1988; Denslow & Gomez Diaz 1990; Thompson et al. 1998). Uhl et al. (1988) found advance growth accounted for 97 % of all trees ≥ 1 m in single-tree falls and 83 % in multiple-tree falls. Almost all trees in both gap types were from species classed as climax. Furthermore, in this study, advance growth had much lower average annual mortality over four years than individuals germinating after gap formation.

Even in large gaps, advance growth can play a vital role for some species. In Puerto Rico, regeneration of the climax tree *Manilkara bidentata* after a hurricane relied upon advance growth to re-establish the site because 60 % of its seedlings smaller than 15 cm were buried and killed by litter and adult trees took at least nine months to recover from the hurricane before fruiting again (You & Petty 1991). Similarly, resprouting trees and surviving advance growth seedlings of climax species dominated regeneration after a large hurricane in Nicaragua (Yih et al. 1991).

Species with large seeds and seedlings regenerate more often from advanced growth and seed rain than from the seed bank (Devoe 1992; Martinez Ramos & Soto Castro 1993). A large seed size enhances the ability of seedlings to survive longer under closed-canopy, understorey light conditions. Larger seeds tend initially to produce larger seedlings which have better developed root systems to withstand desiccation, improve mycorrhizal infection, and persist in the shade of the closed forest than small-seeded seedlings (Ng 1978). Furthermore, these plants are more able to survive the shock associated with gap creation and, with larger leaf areas than species initially producing smaller seedlings, can grow more rapidly upon gap creation (Uhl et al. 1988; Brown & Whitmore 1992). In addition, a large seed may enhance a species' ability to attract large animal dispersers (Grubb 1996).

The gap environment is transient. The microclimate at seedling height can return to pre-gap levels within a few years of gap creation in tropical forests (Denslow 1987; Fraver et al. 1998), depending upon the size of the canopy opening. Consequently, most plants must spend a large part of their lives in the shade of the closed-canopy forest. Canopy species typically go through multiple episodes of gap-release then suppression before reaching the canopy (Becker & Wong 1985; Brokaw 1985b; Uhl et al. 1988). Hence, species regenerating through advanced growth are better equipped to persist and grow slowly for long periods under canopy shade, and have a large initial size advantage over species whose members establish after gap creation.

Brown and Whitmore (1992) found that above all other factors, such as response to light, etc., survival and growth of all individuals in gaps was greatest for the largest seedlings already present as advanced growth. In that forest, species that had a large proportion of large seedlings as advance growth had substantial competitive advantages irrespective of gap size. Note, however, that the relative importance of advance growth compared to seed rain and the seed bank in a forest will depend upon the type, frequency and intensity of disturbance (Connell 1989).

Although advance growth may remain under the shaded canopy for many years until a gap opens, the population of seedlings and saplings is not static. In some forests, mortality of advance growth is high (Martinez Ramos & Soto Castro 1993), but continuous, low-level recruitment of climax species from the seed rain replaces mortality. Thus, the population in absolute numbers may remain similar but turnover may be high (Runkle 1989).

The population of advance growth at a site appears to be structured by an interaction of species biology (seed size, seedling morphology and physiology, including shade tolerance), biotic interactions (mycorrhizal relationships, seed dispersers, pathogens, and herbivores), and stochastic factors such as drought (Bazzaz 1991; Martinez Ramos & Soto Castro 1993). As vertebrate frugivores are the main seed vectors in most tropical rainforests (Terborgh 1990), frugivory plays an important role in advance growth dynamics (Martinez Ramos & Soto Castro 1993). Brokaw and Scheiner (1989) stressed that more detailed research is needed to address the dynamics of advance growth populations, especially advance growth populations beneath a mature closed canopy since this is where individuals live most of their lives.

- **Sprouting**

Re-sprouting from broken stems or roots is very important for regeneration in some forests. Sprouting has been reported as a dominant re-establishment mechanism employed by tree species after large disturbances such as hurricanes (Walker 1991; Yih et al. 1991; Bellingham et al. 1994), as well as following very small disturbances (Arevalo & Fernandez-Palacios 1998). Kennedy and Swaine (1992) and Thompson et al. (1998) found high sprouting rates in saplings and trees in artificially created gaps where trees and saplings were topped at two metres. In the latter study, sprouting ability decreased with increasing stump diameter; palms did not sprout.

Plant growth

Generally, height growth increases in gaps or higher light areas compared with closed forest, and early-successional species tend to grow faster in high light areas than late-successional species (e.g., Uhl et al. 1988; Oberbauer et al. 1989; Turner 1990b; You & Petty 1991; Amezquita 1998; Fraver et al. 1998; Luizao et al. 1998). Nevertheless, among species are long continua of light tolerance based on their physiological growth modes. For example, four similar *Shorea* climax tree species from Sri Lankan rainforest showed clear differences in survival and growth on different topographic and light micro-environments, related to the availability of soil moisture and light (Ashton et al. 1995).

Small absolute light changes can produce large differences in leaf gas exchange and carbon allocation of some species (Oberbauer et al. 1993). Plants can also react differently based upon factors such as nutrients, water balance, and litter level. In greenhouse trials, seedling growth optima of a broadly sun-tolerant species (*Flindersia brayleyana*) depended upon interactions between light and nutrients, with growth optima and tolerance to light increasing with increased nutrient availability (Thompson et al. 1988). Nutrient availability may limit growth of shade-tolerant species in low light (Burslem et al. 1996). However, in a comparison of gaps and closed forest, results from Luizao et al. (1998) did not support an interaction between enhanced light and nutrients with respect to plant growth in gaps.

Garwood (1996a) reviews tree-seedling morphology including aspects related to establishment and growth. Bazzaz and Pickett (1980), Bazzaz (1991), and Kitajima (1996) review the physiological responses of plants to increased light and gaps,

including their growth responses. In five co-occuring Moraceae species in Mexico, Strauss-Debenedetti and Bazzaz (1991) found that early-successional species had higher plasticity and photosynthetic acclimation potential than later-successional species.

Seedling health and survival: biotic interactions

Differences in plant composition and dynamics between gaps and closed-canopy forest reflect not only changes in the micro-environment and inherent morphological and physiological characteristics of a species, but also how each individual plant interacts with other organisms in its surroundings.

A determinant of seed and seedling mortality is distance and density dependence. The escape hypothesis (Janzen 1970; Connell 1971; reviewed in Howe & Smallwood 1982) predicts that seeds and seedlings will suffer less predation dispersed away from conspecific adults than under them because of concentrated feeding under a fruiting parent tree by specialist predators. This has been demonstrated to varying degrees for different species and forests (Augspurger 1984b; Connell et al. 1984; Becker 1985; Sork 1987; Schupp 1988b; Kitajima & Augspurger 1989; Peres et al. 1997). Clark and Clark (1984) also found evidence for density and/or distance dependence. However, their study and studies they reviewed showed that seedling mortality often was not from host-specific predation as was originally proposed. Intra-cohort competition, allelopathy, higher frequencies of destructive litter-fall from the adult canopy, local depletion of nutrients around adult root zones, or strong crown shading were other causal factors. Hammond et al. (1999) found that distance from an adult tree could affect the timing of seed attack rather than the total number of seeds attacked, giving the seeds more time to germinate and establish as seedlings before attack.

Mortality patterns differ strongly with species and between life history and size classes (Chapman & Chapman 1996); they are not constant, but are strongly dependent upon the habitat in which an individual occurs (Schupp & Frost 1989). Seedling survival is often higher in gaps than in closed forest (Augspurger 1984b; Sork 1987; Cintra & Horna 1997; Amezquita 1998). Therefore, occurring in a gap can be more important for seedling survival of some species than being away from a parent (Cintra & Horna 1997). Generally, the mortality rate for a species decreases with increasing plant size (Clark & Clark 1992; De Steven 1994), although in relative terms, mortality

due to physical damage becomes more important and pathogen-induced mortality less important with increased plant size (Clark & Clark 1991).

Augspurger (1984b) found that seedling mortality from pathogen attack formed the largest fraction of early seedling mortality under shaded conditions, but pathogen mortality was reduced in light gaps even when seedlings occurred in high densities. This benefit may be a prime advantage of dispersal into gaps: to improve early seedling establishment. However, pathogen-produced mortality as well as density-dependent mortality of young seedlings was very species-specific. Some species were highly vulnerable to pathogens even at low density while other species were not vulnerable even at high densities (ibid). Young seedlings of early-successional species were more prone to pathogen-induced mortality than later-successional species (ibid.).

Herbivory of seedlings is species-specific. Herbivory of rapidly growing pioneer species by insects on Barro Colorado Island, Panama, occurs four times faster in the dry season and ten times faster in the wet season than herbivory of slow-growing climax species (Coley 1996). Young leaves tended to suffer higher rates of herbivory than mature leaves. Nevertheless, total levels of herbivory may be more on leaves in the closed canopy than in gaps as an artefact of their duration and the consequent increased exposure (Newberry & de Foresta 1985). In that study, a higher level of phenolic (defence) compounds found in leaves of plants in gaps than in closed-canopy was thought to reflect greater metabolic rates associated with higher light rather than specific herbivory defence since polyphenolics are also needed for structural growth.

Chance (stochastic events)

Chance plays an undefined role in the survival of seeds, and establishment and growth of seedlings to reproductive adulthood. Despite all the abiotic and biotic factors shown to determine species composition and abundance in a forest, chance also influences forest structure and dynamics. Hubbell and Foster (1986a) argued that successful growth and survival to maturity of an individual plant may depend as much on being in the right place at the right time as on its individual species characteristics. Other studies have noted that chance operates in forests to varying degrees (e.g., Becker 1985; Brokaw 1987; Whitmore 1989; Brown 1993). The importance of stochastic processes will, like other factors influencing forest dynamics, depend on the species or combination of species involved, the season, and the scale of observation.

2.1.3 Conclusions

The gap phase in a forest is an important focus of plant regeneration, depending upon many complex and interacting processes. Gaps are not discrete and homogeneous entities; within-gap heterogeneity of micro-environmental conditions and species composition is high. As such, gaps are difficult or even impossible to delineate. Not only are gap environments highly variable, but closed canopy forest, which is treated routinely as a homogeneous control in gap experiments, is also highly heterogeneous (Lieberman et al. 1989; Lieberman et al. 1995).

Ecologists have commonly characterised plant species into two broad regeneration strategies, that of pioneer/early-successional and climax/late-successional species. These strategies represent the poles of a continuum along which species occur and overlap in their establishment, growth, and survival responses to disturbance. Advance growth is one of the mechanisms by which species can re-establish in a gap. It is favoured by late-successional species. Much more needs to be understood in terms of the dynamics of advance growth populations, covering how they react to long-term life in the closed canopy shade of the forest, and how they respond to gaps.

Increasingly, ecologists are refining or re-evaluating the dichotomous characterisations of regeneration and forest growth (for example, Brokaw & Busing 2000). Dichotomies - gap versus non-gap, large versus small gap, pioneer versus climax species - are useful aides for understanding and interpreting broad forest processes. Nevertheless, tropical ecology has reached a stage where these characterisations could restrict our view of forest dynamics. Gaps are vitally important to the determination of forest pattern and dynamics, but they fit in to the larger forest cycle. For example, although what grows in the area affected by a disturbance determines the species available in later growth phases, equally, species available to colonise a disturbed area depend on pre-gap processes (Brokaw & Scheiner 1989). Similarly, although pioneer species have generally different characteristics from climax species, most forest plants are from species classed as climax, so research within this group is imperative. Hence, new research, such as this thesis, must contribute to a more complex explanation of regeneration mechanisms beyond the broad dichotomies offered in earlier research.

2.2 Natural vs. human-induced forest disturbance

Globally, logging or agriculture degrades large areas of tropical rainforest. Some studies try to address this problem by comparing human-induced disturbance with undisturbed mature forest (e.g., Uhl et al. 1982; Young et al. 1987; Riswan & Kartawinata 1991; Saldarriaga & Uhl 1991; Congdon & Herbohn 1993; Aide et al. 1996; Allum 1996; Pinard et al. 1996; Gardner 1997; Winthrop 1998). Few (Uhl et al. 1988; Uhl et al. 1990; Walschburger & von Hildebrand 1991; Nepstad et al. 1996) examine the differences in regeneration dynamics between what occurs naturally through the gap phase in forest and what occurs in areas abandoned by cultivation or after logging.

In Venezuelan Amazonia, Uhl et al. (1988) examined the impacts on regeneration of removing all advance growth vegetation before (artificially) creating tree-fall gaps. Plots in which advance growth was removed had less than half the woody plant density of paired tree-falls with advance growth intact. In the single tree-falls without advance growth, most colonisers were still primary forest trees whereas pioneers were the most common colonisers of multiple tree-fall gaps.

Walshburger and von Hildebrand (1991) compared naturally created tree-fall gaps with slash-and-burn sites in the Colombian Amazon. Natural gaps were generally <500 m^2, but the cultivated sites were approximately one hectare and had been burned, planted, weeded, and crops harvested. Consequently, natural gaps provided considerably smaller areas of soil perturbation than cultivated sites. The most frequent species in the cultivated sites (pioneers) had very few individuals in the natural gaps and closed forest understorey.

Nepstad et al. (1996) studied regeneration in a large area (10 ha) of abandoned cattle pasture. As Allum (1996) found, sites with intensive disturbance histories recovered much more slowly. Tree seedling and sprouting recruitment was more than two orders of magnitude greater in forest habitats than pasture, which had suffered severe disturbance through being cut, burned, planted, grazed, and sprayed with herbicide, but neither bulldozed nor fertilised. In pastures, low density and diversity of tree seedlings and sprouts was due not only to low rates of emergence but also to disproportionately high mortality compared to forested sites.

Seeds of tree species are extremely rare in the forbs- and grasses-dominated soil seed bank of abandoned pasture (Quintana Ascencio et al. 1996; Zimmerman et al. 2000) or cultivated agro-forest (Gardner 1997), although seeds of late-successional species are seldom represented in seed banks, even in mature forest. In addition to the limited seed availability, dispersed seeds can suffer higher predation rates in pasture because rodent populations are higher there than in the closed forest (Nepstad et al. 1996; Holl et al. 2000; Wijdeven & Kuzee 2000). Nepstad et al. (1996) found seed predation was lowest in forest tree-fall gaps. In that study, seedling herbivory was also higher in the pasture than in tree-fall gaps: several tree species in the pasture had 50-80 % herbivory damage within 16 days whereas herbivory never exceeded 33 % in tree-fall gaps. Larger trees suffered less in all sites. Herbivores preferred tree species in the pasture over grasses or shrubs.

Herbivory effects may be very species- and site-specific on abandoned agricultural sites. For example, taller tree seedlings suffer less mortality due to leaf-cutter ants than smaller ones because they have more resources to replace damaged leaf and stem tissue (Nepstad et al. 1996; Vasconcelos & Cherrett 1997). Hence, herbivory may retard growth of the larger seedlings but is less likely to cause mortality than with damaged small seedlings. This follows from natural regeneration observations that it is always the larger seedlings that survive and gain most from gap environments (Uhl et al. 1988; Brown & Whitmore 1992).

Several generalisations can be drawn from the literature about forest recovery following human disturbance. Firstly, more early-successional tree species colonise following human disturbance than natural disturbance. Secondly, some sites may eventually reach similar forest composition to mature-phase undisturbed forest, but this may take a very long time and depends upon a number of interacting factors. For instance, regeneration depends upon the type, intensity, size, and frequency of disturbance; and time since abandonment. On Pohnpei, Allum (1996) found sakau-cultivated sites differed significantly in species composition and density from mature undisturbed forest. Regeneration was retarded on cultivated sites with delay proportional to the period of cultivation and size of the plot. Frequent disturbance increases the differences in regeneration between undisturbed and disturbed areas. Short disturbance return times result in increased weed species abundance (Quintana Ascencio et al. 1996). In addition to disturbance history, general site conditions (climate, topography and soils), the floristic composition of neighbouring vegetation,

and availability of seed dispersal agents all determine how well the seed bank and advance growth survive, and the proximity of adult seed trees for seed rain.

As disturbance increases in size and/or intensity, mechanisms of natural regeneration are gradually lost (Connell 1989; Uhl et al. 1990; Oliver & Larson 1996). Uhl et al. (1982) found that as human disturbance increased in intensity, new recruitment changed from largely climax forest species (where vegetation was cut), to early-successional woody species on the cut and burned site, to forbs and grasses on the bulldozed site. Aide et al. (1996) found the age since abandonment to be the best predictor of forest stand characteristics. However, like factors affecting gap-phase regeneration in undisturbed forests, the relative importance of factors affecting forest recovery from human activities varies widely.

Tropical deforestation is proceeding extremely rapidly at a rate of 15.4 million hectares per year - 0.8 % of tropical forest area, and 1.1 % of upland (hill and montane) tropical rainforests (FAO 1993). Vast areas of forest lands are already degraded from human activities. We desperately need to accelerate recovery of these degraded forest areas. Understanding the different regeneration pathways following natural and human disturbance will suggest ways of intervening to accelerate recovery of degraded forests towards intact-forest cycle processes.

Chapter Three: Research Outline

Chapters One and Two of this thesis outlined the practical and scientific relevance of my research in Pohnpei's upland forests and the general aim of my thesis. In this third chapter of the introduction are presented the research objectives and definitions for the three types of forest plots delineated in the field research; mature-phase forest, gap-phase forest, and sakau-agro-forest. In particular, I outline why the gap-phase forest plots were created artificially rather than tracking natural gaps. This is followed by an introduction to Pohnpei's upland forests, including a discussion of how Pohnpei's upland forests compare with other, more commonly studied tropical rainforests. Although Pohnpei is normally very wet, the fieldwork for this research was conducted during a severe drought. Pohnpei's normal weather conditions and the 1998 El Nino drought are outlined in Chapter 3.6 to alert the reader to the strong drought effect underlying part of the fieldwork period.

Chapters Four and Five of this thesis cover the field methods and analysis methods, respectively. Thesis results are then presented in chapters six and seven. In Chapter Six, mature-phase upland forest and sakau-agro forest are compared first at the initial (time 0) census along with results from a preliminary forest disturbance survey that outlines the natural scales of disturbance in upland forest. Chapter Seven then tests in detail if and how the plot types changed over 15 months, and compares the initial plant populations censused at time 0 with seedlings that were newly recruited during the following 15 months of the study. Important facets of the results are discussed in Chapter Eight and their implications for restoration of Pohnpei's forests explored in Chapter Nine.

3.1 Thesis Objectives

This research was based on the general hypothesis that:

- **Regeneration on upland forest sites converted to sakau cultivation is retarded compared to regeneration following natural-simulated disturbance in intact forest because of the loss of advance growth through forest clearing and clean-weeding.**

It was predicted that advance growth would be a dominant establishment mechanism for tree species following natural disturbances in Pohnpei's upland forest, but its role in regeneration of abandoned sakau plots would be minor. Species relying upon advance growth for establishment would be excluded from sakau plots.

To test these hypotheses, I sought to identify mechanisms differentiating regenerating populations under the two conditions, and to explore their implications for forest restoration with these objectives:

1. to determine the density, composition, health, growth and survival of advance growth in undisturbed upland forest with a closed canopy (mature-phase forest) and with canopy openings (gap-phase forest), and in areas disturbed by sakau cultivation;
2. to describe and explain gap-phase plant recruitment, survival and growth differences among species and between simulated-natural gaps and sakau-agro-forest gaps over time;
3. to predict future forest composition following sakau cultivation, and suggest practical treatments to alter the regeneration pathway to mimic more closely that of undisturbed forests.

All available plant species were sampled, across size classes, and with measures of micro-environment (light, litter) attached to each of the smallest sample units (quadrats within plots) for analyses independent of the way plot types were delineated. Sampled populations were re-measured three times over 15 months and analysed to track the growth and survival of advance growth with and without natural disturbance and compared with human-induced disturbance.

3.2 Artificially created gap-phase forest

In order to avoid the confounding effects of varying times since gap creation, I did not study natural gaps. Instead, I created experimental gaps by felling selected trees in censused, mature-phase, forest plots.

Artificial gap studies are becoming an increasingly important method of study for gap-phase forest dynamics. First used by Kramer (1933) in Java, they have been used in Venezuela (Uhl et al. 1988), Puerto Rico (Devoe 1990, 1992), and Borneo (Brown & Whitmore 1992; Kennedy & Swaine 1992; Whitmore et al. 1993). Outside very large permanent plot studies where all individuals are tagged and gaps may naturally occur, for example, the 50-ha permanent plot on Barro Colorado Island, Panama, by Hubbell and Foster (1986b), creating artificial gaps is the most practical way to track advance growth individuals from mature-phase forest through into the gap phase.

A preliminary forest disturbance survey provided the rationale for the size of experimental gaps (see 4.1 for methods, and 6.1 for disturbance survey results). The date that a tree or trees was felled in a plot became time 0 for that plot and its closest mature-phase, closed-canopy plot and sakau plot.

3.3 Definition of terms

Plot types:

- **Mature-phase forest, abbreviated to MPF**: refers to plots in intact, closed-canopy, upland broadleaf forest. Note that in results for the initial census, there were 14 plots classed as mature-phase, before seven of them were treated and became gap-phase. Thereafter, MPF refers to the seven plots that began and remained mature-phase. Statistically, this was the control plot type.
- **Gap-phase forest, abbreviated to GPF**. These seven (later six) plots were mature-phase at the initial census but became gap-phase through the felling of trees in each plot to create gaps. Thereafter, they were gap-phase, and were used to follow natural regeneration in upland forest under gap-phase conditions.

Collectively, MPF and GPF plots were termed "forest", to separate them conceptually from sakau plots in the uplands, which were "agro-forest".

- **Sakau-agro forest, abbreviated to SAF.** These were plots sited in areas that were once upland forest, but which were cleared for sakau cultivation for a number of years before abandonment (see plot selection criteria in methods 4.2.1).

Recruitment cohorts:

- **Advance growth/Time 0 cohort:** The advance growth population is assumed to be those plants pre-existing at time 0 (i.e., at the initial, pre-gap census) even though individuals within the population will be of greatly varying but unknown ages. Strictly speaking, advance growth usually refers to the bank of seedlings that sit semi-dormant in the forest understorey until a gap opens and they respond with more active growth. However, for a canopy or sub-canopy species, individuals may go through many periods of different gaps opening and closing, active growth then suppression. Consequently, individuals across several size classes were studied, as saplings too may be going through these periods of suppression and growth acceleration.
- **New recruitment**: arrived after time 0 gap creations, so are of known ages. Note that I have assumed that SAF cultivation is also at time 0 even though in reality they were abandoned two years prior to time 0.

3.4 Species terminology

Scientific names in this thesis follow Fosberg (dicots: 1979; ferns: 1982; monocots: 1987). Exceptions to this are for *Syzygium* which follow Glassman (1952), and *Lemmaphyllum* (Fosberg 1992). A list of all species recorded in the research plots, their naming authorities, and Pohnpeian names (where known) is in Appendix A. Author names follow the Brummit and Powell system of abbreviation (see: http://www.kew.org.uk/data/authors.html).

At the first citing of a species in the text, the full binomial species name including naming authority is given. Thereafter, species are referred to by their genus name only rather than the genus and species, unless it seems particularly appropriate to give the full name. For example, *Parinari laurina* Gray is hereafter referred to simply as *Parinari*. As most species recorded, particularly the more common ones such as

Parinari, were the sole species in their genera on Pohnpei, this is appropriate and helps the text flow more easily.

3.5 Pohnpei's upland forests

In general terms, upland forest refers to all the intact indigenous forest occurring in the uplands above ~200 m elevation. However, within the uplands different forest types are recognised. From ~200-450 m is upland broadleaf forest which is the dominant upland forest type (46 % of 1995 intact upland forest was upland broadleaf forest, and 70 % in 1975). From ~450 m the forest is dominated more by palm species (so called "palm forest"), particularly the endemic canopy palm *Clinostigma ponapensis* (Becc.) Moore & Fosberg, until it becomes montane dwarf forest on the ridges of tall peaks. In wetter areas, the ivory-nut palm (*Metroxylon amicarum* (Wendl.) Becc.) is predominant. The lowlands are filled with homes, roads, agro-forest/tree gardens, and secondary vegetation; lowland rainforest is extinct, having been completely replaced through human activity. Mangroves, then the barrier reef, surround the island.

This thesis specifically concentrated on upland broadleaf forest because it is the most common upland forest type and because it tends to occur in the lower-mid upland slopes, the area most affected by current forest conversion. The dominant canopy-tree species in upland forest are *Clinostigma*, *Parinari laurina* Gray, and *Campnosperma brevipetiolata* Volkens (see Chapter Six for a full picture of forest composition and structure). The general forest composition may vary on different soil types and topographies but this has not been examined. Much of the upland forest occurs on moderate to very steep slopes. Research targeted the mature-phase (closed-canopy, mature trees) of upland forest because it is the desired end point of restoration and with manipulation enabled an exploration of the gap-non-gap dichotomy in gap-phase regeneration.

Most of our knowledge on tropical rain-forest regeneration and forest dynamics has come from continental, tropical lowland or hill forests. Although it is certainly valid to compare Pohnpei's forests with these, the reader should keep in mind that as this forest occurs on a small island in the tropical Pacific, Pohnpei's upland rainforest differs from classical tropical lowland or hill rainforest in several regards. Firstly,

canopy height is relatively low in Pohnpei's upland forests: it is usually only 20-25 m to the leafy closed canopy made by *Parinari* and *Myristica insularis* Kaneh.; *Clinostigma* and *Campnosperma*, when present, emerge up to about 35 m. This is shorter than forest tops on the much-studied Barro Colorado Island, Panama (35-40 m closed canopy with emergents above: Leigh Jr & Wright 1990). Also taller is forest at La Selva, Costa Rica (45-55 m to the emergents: Janzen 1983), Manaus, Brazil (30-35 m closed canopy with emergents 45-50 m: Lovejoy & Bierregaard Jr 1990), and Sibiti-Zanaga region, Congo (50-60 m to emergents (Borota 1991, p.75). Forests that are more similar in height are San Carlos, Venezuela (25-30 m to closed canopy: Uhl and Murphy 1981), and particularly the island forests of Puerto Rico (El Verde Tabunuco canopy ~20 m with emergents up to ~35 m: Odum 1970). Secondly, a few canopy species dominate in Pohnpei's upland forest. This is uncommon in tropical lowland rainforest but more common in mountainous forests and on islands (e.g., El Verde forest, Puerto Rico). In fact, Pohnpei's upland forest is like a mixture of characteristics from both lowland and lower-montane forests, but not upper montane forest (see the summary of forest characteristics by Whitmore 1984, p.243).

Another important difference is in the number of forest animals. Except for two bat species (*Pteropus molossinus*, *Emballonura* sp.), no mammals are indigenous to Pohnpei. The flora and fauna of Pohnpei are mostly derived from South East Asia, Indonesia, Philippines, and Melanesia, areas (south-) west of the island rather than from the Eastern Pacific like Hawaii, or south from Australia (Mueller-Dombois & Fosberg 1998, p.23). Following from island bio-geographic theories, the flora and fauna of Pohnpei are fairly depauperate relative to larger islands and islands closer to the Asian continent. Plants and animals have had further to travel to reach Pohnpei, and even further to islands further east like Kosrae, or Kiribati in the Central Pacific.

3.6 Pohnpei's climate and the El Niño drought 1997/1998

Pohnpei normally has a tropical, super-wet climate; at the coast, mean annual temperature is ~ 27 ° C with the average monthly temperature varying by no more than 0.5 ° C (meterological data from Kolonia weather station, summarised in Ashby (1993, p.121)). In an average year, three days are clear, 63 days are partly cloudy, and 299 are mostly cloudy; mean relative humidity is 80-90 % (ibid., p.123). However,

Kolonia tends to be slightly wetter and cloudier than Madolenihmw, the district where study plots were located, because storms tend to arrive more from the north east near Kolonia than the south east (Madolenihmw), and less again on the western (leeward) side of the island. Mean annual rainfall in Kolonia is 4750 mm/year (35 year average, Ashby (1993, p.120)), but at the coast closest to the forest study sites, rainfall is approximately 4000 mm (averaged over 16 years 1981-1997 at Pohnpei Agriculture and Trade School, Madolenihmw, Figure 3.1). Rainfall more than doubles further into the upland interior of the island (Spengler 1990). There is no distinct dry season but January to March tend to be less wet (Figure 3.1).

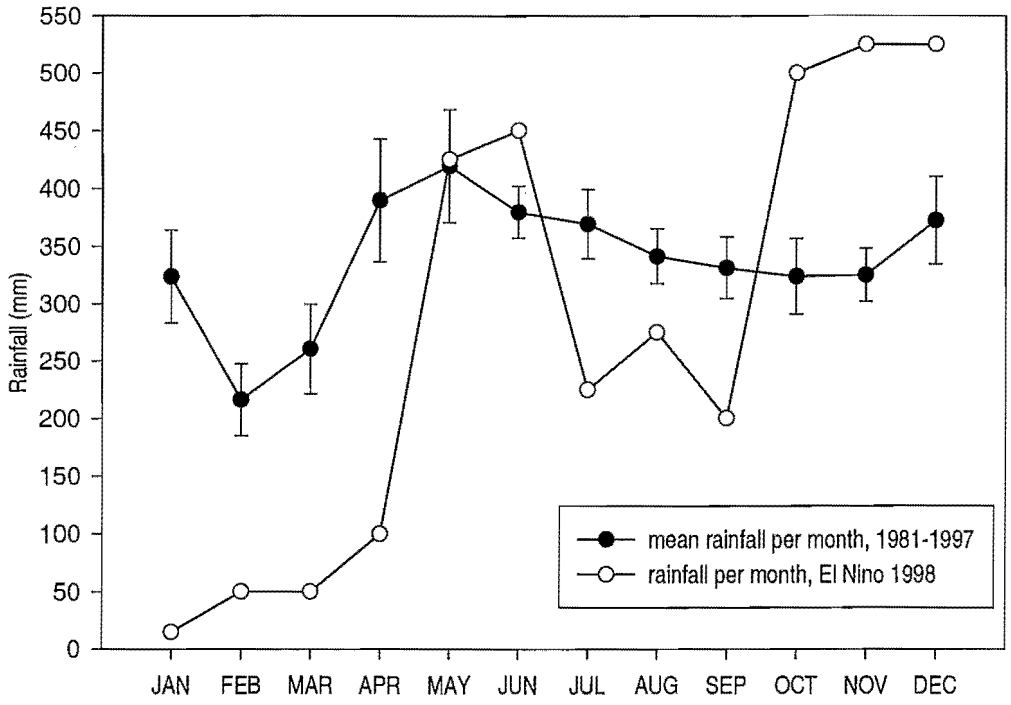

Figure 3.1 Mean rainfall per month (1981-1997) and El Nino year 1998, Madolenihmw.
Source: Miklos Szentkiralyi, Pohnpei Agriculture and Trade School (unpublished).

Other forests classed as super-wet include those in lowland areas of Sarawak, Sumatra, Costa Rica (e.g., La Selva), Venezuela (e.g., San Carlos de Rio Negro), Dominica, Vanuatu, and Papua New Guinea (Richards 1996, p.166).

Although Pohnpei normally has no distinct dry season, the island is periodically affected by the El Niño weather event which is a change in global weather patterns based in the tropical Pacific (see Rasmusson and Wallace (1983)). During an El Niño, rainfall patterns shift eastwards across the tropical Pacific so that the usually very wet,

tropical western Pacific, including Pohnpei, loses much of its rainfall, and the usually dry, central Pacific islands receive high rainfall.

An El Niño drought strongly reduced Pohnpei's rainfall in the first four months of 1998 (Figure 3.1). Rainfall during January to April was only about 18 % of the average rainfall for these four months, and January was less than one percent of its average (data from M. Szentkiralyi, Pohnpei Agriculture and Trade School weather station in Madolenihmw). The main fieldwork period for this research included these drought months. Plots were initially censused in October to December 1997, just prior to the onset of the drought. Thus time 0 data represent normal forest conditions while the one- and three-month re-censuses after gaps were created coincided with the drought months (January to end-April). From May, rainfall returned to high levels for the rest of the year so that the 15-month re-census (May-June 1999) recorded forest recovery and post-drought growth.

In the last two decades, El Niño occurred across the Pacific in 1983, 1988, 1992, and then 1998. However, droughts on Pohnpei in 1988 and 1992 were fairly minor: 1988's driest months still recorded 450 mm rainfall over January to March, 56 % of the 16 year average for those three months, and February to May 1992 received 450 mm, 35 % of average rainfall for those four months. In contrast, the 1982/1983 El Niño was the most severe on record for Pohnpei and one of the most severe world-wide. Total rainfall in coastal Madolenihmw was only 150 mm for five months January to May 1983, which was nine percent of the usual rainfall. The 1982/1983 El Niño strongly affected coral reef communities and fisheries in the Pacific (see related papers in Glynn (1990)). It increased plant mortality in forests in Panama (Leigh Jr et al. 1990; Condit et al. 1995), and especially in East Borneo where there were massive fires (Leighton & Wirawan 1986). Similar drought-induced plant mortality was reported in Sarawak for the 1998 drought (Nakagawa et al. 2000).

Methods

Chapter Four: Field Methods

4.1 Disturbance survey

During September 1997, a brief disturbance survey was conducted in Pehsarep, Sapwalap, Wapar, and Wou Kutoar areas of Madolenihmw plus a small area in Kitti (Figure 4.1). The survey served three purposes: as an introduction to the composition and variability of the upland forest; as a reconnaissance for suitable intact forest sites for the main study; and the disturbance survey itself.

To gauge the frequency of different types of disturbance in upland forest and the size and species of tree(s) that created them, ideally one would have created permanently marked transects and studied decomposition rates for different species and forest turnover from fresh tree falls. However, the area and therefore time required to find sufficient new disturbances and the re-survey periods needed prohibited that approach. Consequently, the following methods were employed and the data interpreted with other observations to select appropriate experimental gap criteria.

Starting from a walking path in the forest, I walked a random compass bearing and searched five metres either side of the transect line for woody debris (although *Clinostigma* fronds were far too numerous and small to record). Debris was classified as uprooted tree, standing-dead tree, large branch-fall from a tree, snapped tree, or sub-canopy tree fall (mostly the tree-fern *Cyathea nigricans* Mett.). The following measurements and notes were recorded: species, log length if a fallen tree or branch, or tree height for standing dead trees; diameter at 1.3 m (dbh) from the base of the tree, or 50 cm from the section end for branches and snapped sections; and distance from the start of the transect as measured with a hip chain. For snapped trees and branches, diameter and stem height of the origin-tree were also recorded. Fall direction was recorded for uprooted trees. For trees, it was noted whether they occurred alone or were with others (shown also by the transect distance). Upon reaching a break in the forest, if the area of secondary vegetation was sizeable, the transect was terminated; otherwise I walked through the disturbance and restarted on the other side.

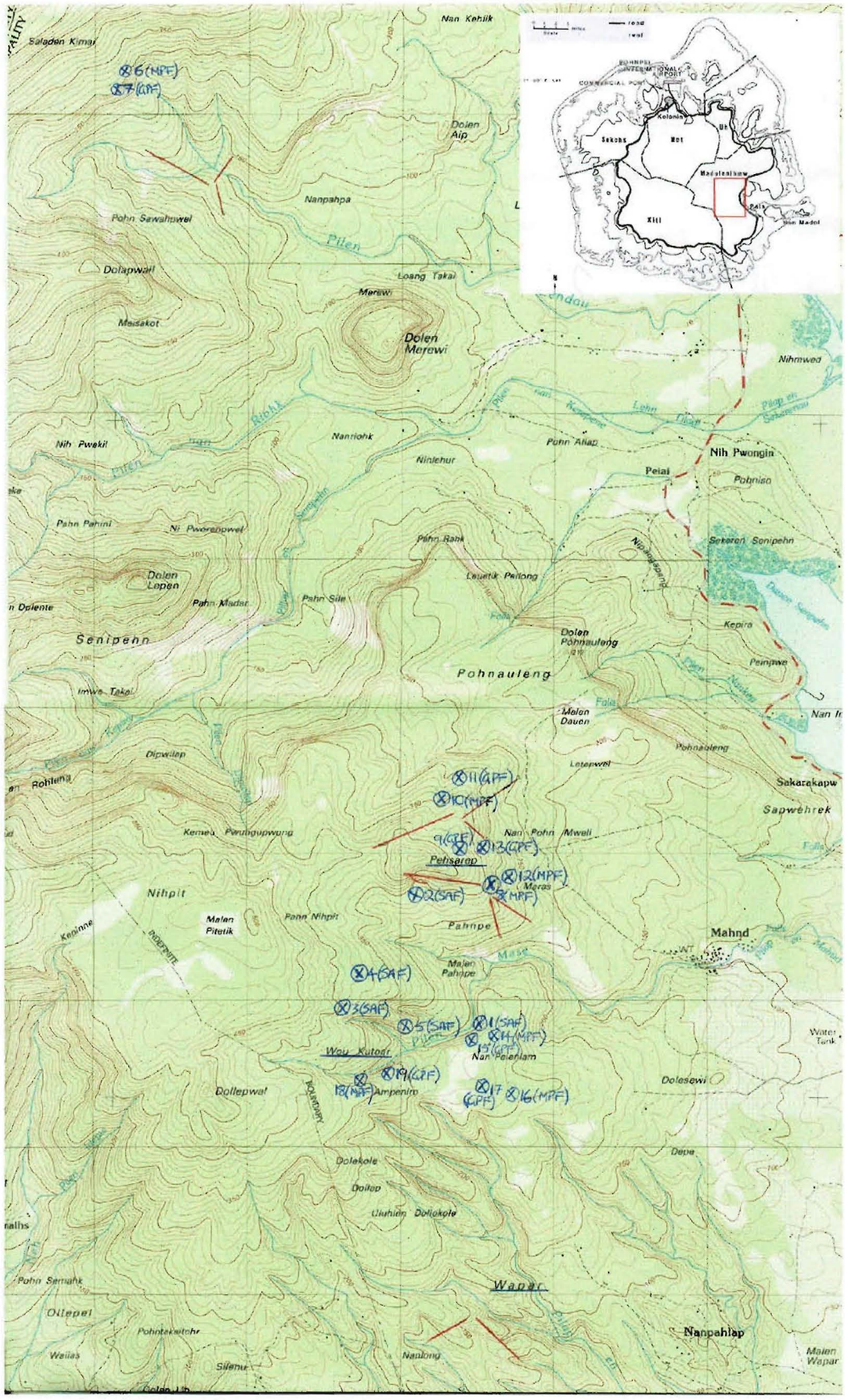

Figure 4.1. Map of study area and location of plots, Madolenihmw.
Approximate location of disturbance survey transects shown in red (Kitti transects not shown). Map scale 1:25 000 (i.e., one square = 1 x 1 km). Inset map adapted from Karolle (1993, p.104); the red rectangle indicates the area shown in the main map.

Gap size was not directly recorded. Instead, the gap maker(s) was studied because it avoided the problem of trying to delimit something that is highly heterogeneous and continuous, and because the gap environment reflects the type and size of the tree(s) that created it.

In total, two hectares were surveyed from 14 transects (2000 m total length by 10 m width) although the area actually walked was much greater than this because we only recorded in intact upland forest. The rate of human-induced disturbance is such that the longest transect was only about 200 m and several were only ~100 m before reaching a cultivated area, either current or abandoned.

4.2 Regeneration following natural and human-induced disturbances

4.2.1 Plot selection

Forest plots

Reconnaissance of forest areas within practical distance from the Pohnlangas forestry station (i.e., preferably no more than one hour's walk from the nearest road-end within Madolenihmw) searched for intact forest areas suitable for sampling. The key selection criteria were for the areas to be mature-phase forest (closed-canopy) with *Clinostigma*, *Campnosperma,* and *Parinari* adults in the canopy, and a high seedling population in the understorey. This forest type best typifies the plant composition and structure of intact upland rainforest in Madolenihmw.

Seven pairs of forest plots (14 plots in total) were chosen (see Figure 4.1 for locations), the number of plots being a compromise between statistical power in significance tests, time, and available forest areas. All forest plots faced east (windward, NE-SE), but plots occurred on a wide range of slopes (Table 4.1). Some plots showed evidence of having more frequent disturbance regimes than other plots, particularly the very steep plots due to their less-stable substrates and conversely the flattest plot (plot 16) because it appeared to be more prone to overland flow. Plot 19 had a more even-sized stand structure of *Parinari* than other plots. It was not possible to locate sites that all had exactly the same forest composition, slope, and with no disturbance. The range of these plots reflects the reality of mature forest on Pohnpei.

Table 4.1 Forest plot descriptions

Plot id	Aspect	Slope	Elevation (m)	Plot type
6	SE	Moderate	420	MPF
7	SE	Steep	400	GPF
8	NE	Moderate	330	MPF
9	E-ES	Slight	370	GPF
10	N-NE	Steep	340	MPF
11	N-NE	Moderate-Steep	320	GPF
12	NE-E	Steep	290	MPF
13	E-ES	Steep	340	GPF
14	E-SE	Slight	290	MPF
15	E-SE	Slight	310	GPF
16	E-SE	Flat	260	MPF
17	SE-S	Slight	290	GPF
18	NE	Steep	350	MPF
19	NE-E	Moderate	330	GPF

Five sakau plots were located in the vicinity of the forest plots (see Figure 4.1). Initially, I had hoped to find seven sakau plots that had been cultivated for only a few years and abandoned within one year. In reality, however, it proved impossible to find plots that fitted those constraints. Under Pohnpei's very high rainfall, the already highly weathered and leached soils deteriorate quickly once deforested. Consequently, growers often produce one to three sakau crops, each crop taking three to about seven years, then leave the site to fallow a number of years before planting the next full crop. Typically, if a grower likes a particular site, s/he will continue to cultivate it until the soil fertility declines appreciably and/or theft of sakau plants - increasingly a problem in some areas - forces abandonment. The revised selection criteria extended the allowable cultivation period but preferred it to be as short as possible; plots were to be on their first rotation since the forest was cut down and abandoned within the last one or two years. Nevertheless, only five plots were found near the forest plots that fitted my criteria and were unlikely to be re-used in the next few years. As far as possible, plots were used where all surrounding vegetation was mature forest, although again, this was not entirely possible in practice because plots were often located within a matrix of disturbed vegetation. The cultivation histories for plots were gained from the

growers (see Table 4.2), and permission received to use their plots for this study. Aspect was unable to be controlled for SAF plots (Table 4.2).

From available soil maps (Laird 1982), soils in the forest and sakau plots were well drained; shallow to deep, depending largely on the slope; loamy, but also very stony in places. Note that growers tended not to site sakau plots on stony or steep sites (Table 4.1, c.f., Table 4.2). All soils were formed in residuum and colluvium derived dominantly from basic igneous rock (ibid.). In US soil taxonomy, soils were associations of fine-very fine, mixed, isohyperthermic Typic Dystropepts; clayey or clayey-skeletal, mixed, isohyperthermic Typic Dystropepts; or isohyperthermic shallow Humitropepts (ibid.).

Table 4.2 Sakau plot descriptions

Plot_id	Grower	Years cultivated	Years since abandonment	Approx. plot dimensions	Aspect	Slope	Elevation (m)	Notes:
1	Raynor family	3	1.5	N-S 38.5 m E-W 32 m	NW	Slight-moderate	250	Only a thin forest strip between S side of plot and N side of neighbour's plot; intact forest on all other sides. A large, dead *Campnosperma* (ring-barked) and a large, live *Myristica* in the NW corner of the plot. Many *Campnosperma* and *Macaranga* saplings; also banana (*Musa* sp.), *Morinda*, *Barringtonia*, and much fern and grass cover.
2	Moses Rudolf	5	2	N-S 32 m E-W 46 m	E-SE	Slight	340	A stream forms the eastern plot border with another sakau plot on the other side. Remnant trees and secondary vegetation surround the other sides, but there are many sakau plots nearby. Some tall *Cyathea* and *Campnosperma* saplings, as well as tall *Sphaerostephanos* and *Nephrolepis* ferns. The plot is mostly surrounded by secondary forest so it may not have been created from primary forest. However, there are many large, recently felled tree logs and some tall trees do still remain.
3	Oknar Rudolf	4	2	N-S 38 m E-W 30 m	SW	Slight-moderate	390	Secondary/regenerating forest along SW border with 50 m to the next sakau plot. *Clinostigma* saplings grow along the NE edge, grading back into *Clinostigma*-dominated forest which surrounds most of the plot. S4 plot is ~300 m to the north.
4	Erlin Alpet	11	2	N-S 50 m E-W 44 m	N-NW	Slight-moderate	370	Tall remnant *Clinostigma* along S edge plus a band of *Clinostigma* saplings (5-8 m tall) within the SE area of the plot. A few remnant trees and secondary vegetation along W and E sides before neighbouring sakau plots. A stream forms the N border (some ivory nut palms, *Metroxylon amicarum,* are growing there), then another sakau plot on the other side.
5	Entrik Etse	7	2	N-S 43 m E-W 39 m	S-SE	Moderate	320	Plot surrounded by a mix of remnant forest and secondary forest, but other sakau plots are nearby. Several large trees were left in the plot - a few *Myristica* along the W side of the plot, several *Clinostigma* and a *Parinari* at the top of the plot, and a bent *Clinostigma* at the S end.

4.2.2 Plot layout

Plots were laid out in the following manner. A centre point was located, which for forest plots maximised the buffer zone to any major disturbance and for sakau plots roughly centred the plot within the cultivated area. The plot centre was marked with a one-metre white PVC pole and flagging. From the centre point, 20 quadrat centres were located using pairs of random bearings and random distances to a maximum radius of 15 m (Figure 4.2a). Each quadrat contained a one-metre square nested within a four-metre square, marked out from the quadrat centre to the diagonal corner points at 90-degree intervals (Figure 4.2b). The one-metre squares were the main surveyed areas while the four-metre squares were used to sample a greater number of saplings and larger trees than would have been available in only the small squares. If two quadrats overlapped, the last one was discarded and new pairs of random bearings and distances were tried until one fit. Usually about four quadrat-location pairs were tested for each of the last five quadrats in the plot.

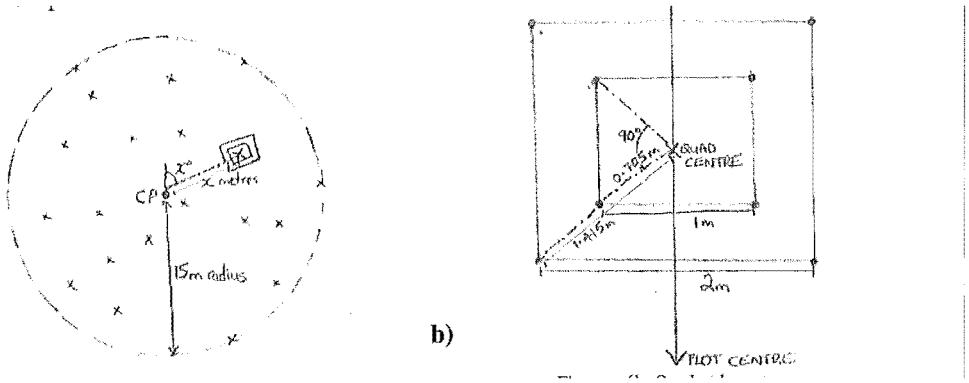

Figure 4.2 Layout for plots (a) and quadrats (b).

Quadrats were marked with plastic knives and flagging at the quadrat centre and the corners of each one- and four-metre square. Plastic knives were used because although they can break if debris falls on them, with almost 3500 corner and centre pegs required, metal stakes were prohibitively expensive and too heavy to carry to most plots. Also, the thin edge of plastic knives allowed more accurate placement at corners than wider stakes when solid roots and rocks were in the way. Flagging was wrapped around the larger square and sometimes the smaller square.

4.2.3 First census (Time 0)

Measurements taken

Forest plots were censused from November to mid-December 1997. Sakau plots were censused mid-December 1997 to mid-January 1998 during the period that GPF gaps were created. Measurements and descriptions were taken at the plot level for summary notes (aspect, slope, elevation, dominant vegetation, and surrounding vegetation), and at the one-metre-square quadrat level. For each one-metre-square quadrat, I described percent litter cover, litter type, measured litter depth with a ruler in six-eight different places, and counted the number of tiny seedlings that were less than 5 cm tall, the height threshold for individual records. Light measurements were taken mostly on a sub-sample of plots or quadrats (see light measurements section, this chapter).

Within each quadrat, all trees and shrubs rooted in the one-metre square that were at least 5 cm tall plus any growing above ground in the square (for example, on buttressed roots of large trees), and all trees and shrubs at least 1 cm diameter at 1.3 m (dbh) in the 4 m^2 (or greater than 1.5 m tall for monocots), were identified to species and tagged. For large trees, pre-numbered metal tags were nailed part way into the stem just above dbh. Seedlings and saplings were tagged with write-on aluminium tags (coded for plot number, quadrat number, and individual number within the quadrat) and tied loosely around the plant with aluminium wire. Where seedlings were quite small, usually those less than 15 cm, tags were anchored to the ground with plastic forks through the wire to prevent tags washing away in heavy rains. All tagged individuals were then measured for height, diameter where dbh was at least 1 cm, and categorised for health status.

While censusing the first sakau plot, it became evident that the high concentrations of grasses, vines and ferns prohibited tagging all individuals. Identifying where one individual of a rhizomatous species became a new individual was too difficult in the time available. Consequently, vines, ferns, and monocots were only recorded as percent-cover-per-species-per-one-metre-square quadrat; no heights were measured. The exceptions to this were *Cyathea, Pandanus cominsii* var. *micronesicus* B.C. Stone, *Clinostigma, Alpinia carolinensis* Koidz., and *Marratia. Clinostigma* and *Alpinia* were measured for height only; the others were measured both for height and scored for percent area coverage.

- **Heights**

For dicotyledonous plants, height was measured to the highest growing bud or piece of live stem in the case of bent plants (Figure 4.3).

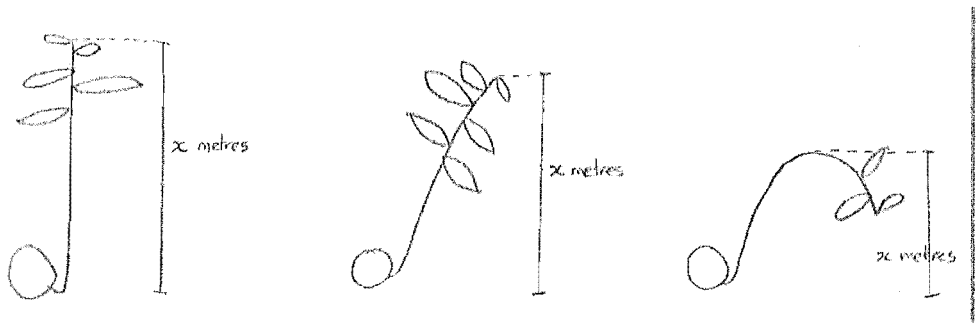

Figure 4.3. Height method for measuring dicots
(illustrated for *Parinari* seedlings).

Where height was measured for monocotyledons and ferns (*Cyathea, Pandanus, Clinostigma, Alpinia,* and *Marratia*), it was to the highest surface (Figure 4.4a). For adult *Clinostigma* palms, *Pandanus* and *Cyathea,* height was also measured to the top of the stem/base of the fronds (Figure 4.4b).

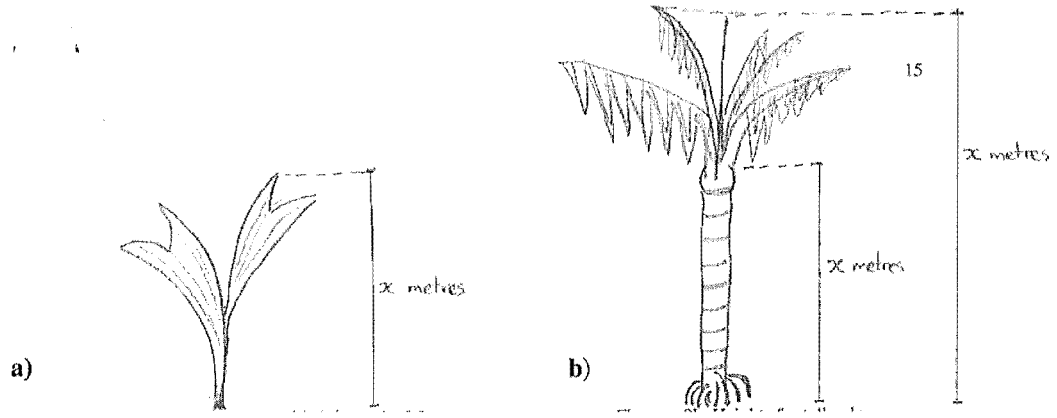

Figure 4.4 Height method for measuring monocots and ferns.
a) general method, b) method for tall *Clinostigma, Pandanus,* and *Cyathea.*

All heights to 1.75 m were measured with fold-up rulers and a short plastic ruler to run level from the top of the plant to the ruler. For the first census, sapling heights less than 6 m were measured with a combination of a three-metre ruler and a marked wooden pole, or occasionally from tree climbing. This method was awkward and very time-consuming so a telescopic height pole was used for the re-censuses. For heights taller than 6 m at the first census and greater than 8-9 m for re-measurements, a Suunto clinometer was used. However, the suunto is inaccurate for heights less than 7 m (manufacturer's guidelines). Consequently, if there were discrepancies between the

heights originally measured with the clinometer and heights where the telescopic height pole could be used (i.e., less than 8-9 m), the height pole measurement was taken as the original height.

- **Diameters**

Diameters were measured where plants were at least 1 cm at 1.3 m from the base of the stem. For trees with stilt or large buttress roots, 1.3 m was measured from the base of the stem above the roots. Likewise for large *Clinostigma* palms, diameter height was measured from above the aerial root skirt. Heights for diameters were permanently marked with heavy marker pen for saplings, or flagging for larger trees. Diameters between one and 20 cm were measured with a set of calipers; a cloth diameter tape was used for diameters greater than 20 cm.

- **Health**

To gauge the change in health of individuals throughout the study, the following health codes were used and notes recorded for each individual:

00 default, very healthy

02 Insect damage, usually to the leaves

03 Fungal damage

04 Stringy hyphae of black fungi (species not known) entangled through plant

05 Plant bent 45 degrees or greater –

-either "covered" (bent over by debris) with debris type noted or, "uncovered" (bending not directly due to debris loading)

06 Loss of central leader

07 Physical branch damage

08 Physical leaf damage

09 Lichen/epiphyll coverage (mostly on leaves)

10 Moss coverage on leaves and/or stems

11 Debris-loading – plant not bent but covered by debris (debris type noted)

14 Wilting during drought months

Dead

Codes 02, 03, and 07-10 were rated on coverage - slight (less than 25 % area covered/affected), moderate (25-50 % cover) or heavy (more than 50 % area cover). Some of the above categories clearly involve damage to the plant's health such as the physical damage. Others, for example, lichen cover, may or may not significantly affect plant health but were recorded nevertheless.

- **Epiphytes**

All observable epiphytes and vines growing up trees were identified to species, described for height presence up the tree (for example, 0-1 m), and estimated for their number, size (small, medium, large) and percent coverage of the tree (if greater than 5 %). Exceptions to this were woody species growing on trees within the one-metre squares, which were censused individually.

- **Light measurements**

Spherical densiometer: In all quadrats, four spherical densiometer readings (see Lemmon 1957) were taken from the four sides of the one-metre-square quadrat facing inwards over the centre point approximately one metre above the ground.

Hemispherical photographs:

In a sub-sample of plots (two plots per plot type), hemispherical photographs were taken one metre above the ground at the centre of each quadrat. GPF plots were photographed before and after felling.

A Nikon FM2 camera with a Nikon Nikkor 8 mm fish-eye lens (f.2.8) and 400ASA Kodak T-max black-and-white film were used. Photographs were taken either when it was evenly overcast or, if clear, when the sun was not shining directly into the plot, that is, early morning and late afternoon. The camera body was mounted one metre above the ground with a tripod, levelled, turned to face true north, a red light-emitting diode shining just at the edge of the lens to indicate direction, and fixed on infinity setting. Photographs were bracketed to cover one underexposure, one correct light, and one over-exposure, each with and without a red filter. The date, time, film number, aperture and light reading were noted for each exposure. Films were sent

to New Zealand for regular black-and-white processing at the University of Canterbury.

The photograph negatives were analysed by GEMlab, University of Kansas, USA, for direct site factor (DSF) and indirect site factor (ISF) (both cosine corrected) which are estimates of the proportion of direct sunlight and diffuse skylight, respectively, under a plant canopy relative to that in the open (Rich 1989). Direct sunlight penetrates down through a canopy opening when the opening is in line with the sun (i.e., sunflecks) whereas diffuse (or indirect) skylight is light entering a canopy that is scattered off the atmosphere (ibid.).

I intended to supplement light models used in the photograph analysis programme with measured data of global and diffuse (under a shadow band) radiation from two photo-diodes (type PH-201a, Nippon Electric Company, Tokyo) mounted on a flat roof at the accommodation base in unobstructed light. Unfortunately, location and technical difficulties during the eight months of measurements meant that there was no reliable set of diffuse radiation data. Consequently, theoretical estimates of radiation data were used instead of measured data in the hemispherical photo analyses.

Light-sensitive papers:

The densiometer and the hemispherical photographs measured light at one metre above the ground, that is, about the average height for *Parinari* seedlings, which were the majority of seedlings recorded. To test for differences in the light environment for seedlings with that of taller seedlings and saplings, light-sensitive diazo paper (ammonia-respondent blue-print paper) was set up following the methods of Friend (1961). A sub-sample of ten randomly chosen quadrats in each of two SAF, two GPF and two MPF plots, was used. For each sampled quadrat, four blackened petri dishes, each with ten layers of regular (g8) diazo paper and sealed with black waterproof tape, were tied across a horizontal bar on a wooden pole and set out for 24 hours. Two pole heights were used: 1 m and 3 m (Figures 4.5a and b, respectively). Uniformly clear and dry days were chosen. This work was completed during the El Niño drought months (see drought section 3.6), which were characterised by hot, sunny days.

a b

Figure 4.5 (photo): Measuring light using light-sensitive diazo papers
Photo papers are a) 1 m, and b) 3 m off the ground.

Paper stacks were kept in black plastic with dehydration crystals until they could be developed in ammonia and the number of bleached papers and part-papers counted (see Friend 1961). The four measurements on each pole were then averaged.

4.2.4 Gap creations

One plot from each forest pair was randomly chosen to become a gap plot. In each gap plot, a medium-large hardwood tree was selected (30-60 cm dbh, > 20 m height; see disturbance survey results 6.1 for rationale). The difficulty in finding suitable intact forest sites meant that plot centres were located to maximise buffer distances between a plot and forest edges with agro-forest, so trees to be felled were chosen after site layout. The tree to be felled (e.g., Figure 4.6) was located near the edge of the forest plot and felled towards the plot centre so that the full length of the fallen tree was laid out within the plot.

In the seven to-be-gap plots, three gap initiators were *Myristica*, two were *Campnosperma*, and two *Parinari*. In all but one plot, secondary trees were knocked down when the gap initiator was felled. If a smaller tree was directly in the fall path of

the main tree, it was sometimes felled first and the larger gap initiator felled over top of it. *Clinostigma* was the most common secondary tree but fell underneath the larger gap initiator so it seldom increased the gap size. Densiometer measurements and hemispherical photographs were retaken in the felled plots.

Figure 4.6 (photo): Felling a selected *Campnosperma* tree in plot 19.

Fellings were spaced over six weeks 29 December 1997 to 9 February 1998 to allow time for the plots to be re-censused on schedule. For experimental purposes and since the pre-felling census and the tree felling were relatively close in time (i.e., within two months), they were treated as effectively the same time. Thus, the census clock time for a GPF plot and its MPF pair was reset to time 0 at its felling date. Sakau plot time 0 was taken as the time the initial census for each sakau plot was completed (mid-December to mid-January).

It was intended that forest plots would be blocked with sakau plots to form triplets, that is, one MPF plot, one GPF plot, and one SAF plot, to help control for variation in plot location (slope, aspect, soils, forest structure). However, logistical constraints meant that sakau plots were selected after forest plots had already begun to be censused. Blocking with forest plots proved to be unfeasible because suitable sakau plots were so difficult to find and, once found, they were not located close enough to the forest plots. Even among the so-called forest-plot pairs was very high among-plots variation, partly inherent and partly from the difficulty in finding similar enough sites for paired plots. Preliminary statistical analyses (not presented) showed that blocking among forest plots was insignificant for all measured variables at time 0 except for canopy openness. Consequently, blocks were abandoned and the design treated as a randomised plot allocation.

The initial blocking meant that plot allocations between MPF and GPF followed a restricted random design rather than completely randomised because a GPF plot was chosen out of the two plots in a forest pair rather than seven chosen from 14 plots. Nevertheless, it was very fortuitous in practice to have MPF and GPF pairs because as the El Niño drought progressed the plots that were re-censused later into the drought tended to show the greatest mortality. Felling of GPF plots was originally spaced to allow sufficient time at each re-census for a gap, its mature-forest pair, and a sakau plot. Consequently, drought effects were evenly recorded among the plot types.

Plots were re-censused one, three, and fifteen months after time 0. The one-month re-census gauged immediate changes in litter and seedling numbers in the GPF plots post-gap compared to MPF. The three-month re-census was designed primarily to examine short-term seedling growth, survival, and recruitment patterns among the plot types, and was the last re-census opportunity during my first visit to Pohnpei. Plants were re-censused at 15-months during a second trip to Pohnpei in April-May 1999. It was hoped that after 12 months under Pohnpei's normal rainfall (i.e., no drought), regeneration differences among plot types would be significantly detectable, particularly in new recruitment and seedling and sapling growth.

4.2.5 One-month re-census (Time 1)

One month after time 0, each GPF and MPF plot was re-censused for changes in litter, tiny seedlings, and survival and health of existing individuals. Any new plants were tagged and measured using the initial census methods. Sakau plots were not re-censused at one month because changes would be undetectable (a preliminary re-census of plot S1 showed that less than 5 % of the plant population had changed).

4.2.6 Three-month re-census (Time 2)

Three months after each felling, or the initial census for sakau plots, plots were re-censused using the initial methods except that the following measurements were not retaken because no differences would be discernible over three months or the information was not needed:

- Large tree heights (those taller than 8 m)
- Diameters
- Epiphytes
- Heights for monocots, ferns and vines in the forest plots, apart from *Clinostigma, Cyathea, Pandanus* and *Alpinia.*

4.2.7 Fifteen-month re-census (Time 3)

Fifteen months after time 0 and one year after the previous census (time 2), plots were re-censused for:

- Height and diameter of all surviving trees and shrubs < 10 m
- Percent cover for non-woody and liana species
- Identification and census of new recruits
- Litter depth (but not leaf-litter cover).

4.2.8 Plant specimens

Plant specimens were collected when species flowered and/or fruited, and dried in a plant press kept in a slow oven. Because of the drought, many species did not

flower or fruit until the rain began to return in April; others still had not flowered by late May at the end of the first field trip, but most were collected during the 1999 trip. On the second trip, I also collected small samples of seeds for tree or shrub species found fruiting that were needed for seed mass data.

All but two specimens were identified to genus and most to species (see Appendix A for a complete list of species recorded)[8]. Vouchers were deposited with the herbarium at *Manaaki Whenua* Landcare Research, Lincoln, New Zealand.

[8] In addition to the two unidentified specimens, four other rarely recorded species were not identified; specimens for them were either not collected, or the quality of the dried specimen was not good.

Chapter Five: Analysis Methods

The aim of the analyses was to compare forest regeneration with regeneration in sakau-agro-forest, and to gauge the role that advance growth played in these two conditions. Essentially, I wanted to create a picture of "15 months in the life of natural- and sakau-disturbed- forest on Pohnpei" by describing the study areas at time 0 and following them over the next 15 months through repeated censuses. To do this, I:

I. Compared attributes of each plot type at time 0. Gap-phase forest (GPF) and mature-phase forest (MPF) were theoretically identical at time 0 before gaps were created in GPF because they came from the same population of mature-phase, closed-canopy forest.

II. Compared plot type responses over the 15 months of this study. Interactions between plot types and species or species-groups were important here to discover species-(group) differential responses and plot type preferences. I also compared the time 0 cohort (those present at the time 0 census pre-gap), with new recruits (plants arriving after time 0), plus the interactions of these recruitment cohorts with plot types and species-(groups).

III. Examined relationships between different variables or sets of variables for mechanisms underlying any plot type and species-(group) differences.

Statistical procedures used for analyses I and II were analysis of variance (ANOVA), time-series ANOVA, log-linear modelling, G-tests, correspondence analysis (CA), and discriminant analysis (DA). Analyses III used Spearman's rank correlations, regression analysis, canonical correlation analysis (CCA), and de-trended correspondence analysis (DCA). Sections 5.4 (for analyses I and II) and 5.5 (for III) outline how each statistical test was applied.

All analyses used plot type totals for count or proportion analyses, for example, stem frequencies, and plot means for all continuous variables since plots were the main independent units of replication in the study. Exceptions to this were for comparisons between variables (or sets of variables) such as light vs. height growth that involved seedlings ($\leq$ 1.0 m height) that occurred within the 1 m^2 quadrat. Quadrat-level data

was used in addition to plots here because arguably each one-square-metre quadrat in a plot was independent of all others at the scale of a seedling or small sapling. Also, it was at this scale that micro-environmental variables were measured so the quadrat-level examination of relationships provided a better picture of the heterogeneity within the forests.

Computerised statistical analyses were carried out using The SAS System for Windows, release 8.01 (SAS Institute Inc., 1999-2000). The only exception to this was de-trended correspondence analysis that used PC-ORD Multivariate Analysis of Ecological Data, Version 3.0 for Windows (MjM Software Design, 1997).

5.1 Data standardisation for quadrat numbers

At time 0 there were seven plots (140 quadrats) each of MPF and GPF, and five plots (100 quadrats) of SAF. Some quadrats were later destroyed: one whole GPF plot was burnt in a fire, and from each plot type between one and four quadrats was removed due to interference by people walking through the area. By the 15-month re-census, there were 138 quadrats in seven plots of MPF, 119 quadrats in six plots of GPF, and 96 quadrats in five plots of SAF. Consequently, I used only quadrats still viable at the 15-month re-census in analyses.

Equivalent plot and quadrat numbers were not imperative for continuous data analyses because they compared mean responses. For frequency analyses that compared absolute counts of plants per plot type, however, plot type numbers were first standardised to an equal area of 100 quadrats[9] from the number of quadrats viable at 15 months (MPF *(100/138), GPF *(100/119), and SAF*(100/96)). For time-series comparisons where interactions with plot types were compared rather than the main effects, and for comparisons of proportions (e.g., frequency at t_{n+1} / frequency at t_n), raw frequencies were used so as not to lose data resolution by reducing the frequency scale. Plant counts were still presented in tables and graphs in the results after being standardised to 100 quadrats. Results using raw data in proportions or where interactions were of main interest were usually very similar to standardised results.

5.2 Parametric test validity[10]

All ANOVA tests (including multiple/time-series ANOVA), discriminant analysis, and canonical correlation analysis are classed as parametric tests. To be valid, parametric tests require normal data distributions and homogeneous variance structures. Plot means (or sums for frequency data) for each plot type for all continuous, percentage, and frequency variables analysed in this study were well within the bounds of normality in Shapiro-Wilk normality tests (PROC UNIVARIATE in SAS), but variances were not very homogeneous (comparison of box plots in PROC UNIVARIATE). Specifically, variance in SAF was different, usually greater, than MPF or GPF, presumably because one SAF area could encompass remnant forest patches right through to very open grass- and fern-cover. If quadrats were used, the normality was sometimes questionable but variances were more homogeneous.

To improve the normality and/or homogeneity of variances for frequencies when used in analyses with continuous variables, and percentages, data were transformed by the **square-root** and **arc-sine**, respectively. Preliminary tests with quadrat height data showed that transforming by natural logarithms did not change normality appreciably so they were left untransformed.

Square-root transformation: Frequency data often tend toward a poisson distribution wherein the mean and variance are the same. In these circumstances, a square-root transformation helps make the variances more independent of the means (Sokal & Rohlf, 1995), improving the homogeneity of variances and normality of counts. Shapiro-Wilk tests showed that my plot counts data were more normally distributed after transformation although, with the exception of total new recruits, none of the raw frequency measures deviated significantly from a normal distribution originally. Variances among plot types were more homogeneous after plots were transformed. Transformation improved quadrat-level data normality for standing-stock frequencies at time 0 and 15 months, particularly for MPF and GPF. New recruits and mortality, although improved, were still classed as significantly non-normal in the

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[9] The 100-quadrat (rather than 96) standard was chosen for simplicity. MPF and GPF quadrat numbers were scaled down towards SAF's rather than up to GPF quadrat numbers or to per hectare values so that the data were not artificially expanded beyond their measured scales.

[10] Note that tests more specific to categorical data like log-linear modelling, G-tests, correspondence analysis, and chi-square, are not based on normal distributions so they do not require the same assumptions as parametric tests.

Shapiro-Wilk normality tests ($p < 0.05$). Variances were fairly homogeneous for quadrat data.

Arc-sine transformation: For all variables measured as percentages, for example, canopy openness and cover of non-woody species, data were first transformed by arc-sine, known also as the angular transformation:

Arc-sin (Y) = $\sin^{-1}(Y^{0.5})$.

Variances of means at both tails of a percentage distribution tend to be smaller than variances of means near the middle of the range (i.e., 30-70 %). The arc-sine transformation is often used to remedy this skew by stretching out both tails of a distribution and compressing the middle (Sokal & Rohlf, 1995). Normality and variance structures improved through transformation for both quadrat and plot-level data, but according to the Shapiro-Wilk test, quadrat-level data were still fairly non-normally distributed.

Although the data deviate somewhat from parametric test assumptions, particularly in the heterogeneity of plot-level variances and non-normality of quadrat-level means, I chose to use mostly parametric tests, but with a reduced significance level from that normally employed, 0.05, to 0.01. Univariate ANOVA itself is generally considered robust and holds well under deviations from its assumptions. Although non-parametric test procedures now are often almost as powerful as parametric ones (SAS Institute Inc. 1989, p.27), where parametric test assumptions hold even approximately, as I argue is the case here, the ANOVA is still considered the more powerful procedure for detecting departures from a null hypothesis (Sokal & Rohlf, 1995). Using a conservative significance level throughout the thesis decreased the possibility of falsely rejecting the null hypothesis. Also, non-parametric tests in lieu of ANOVA are asymptotic in nature, and on that basis are not recommended for when sample sizes are fairly small (SAS Institute Inc. 1989, p.1196) as could be the case with my plot-level analyses. Non-parametric Spearman's rank correlations were used for most quadrat-level analyses because the sample sizes were large and most data were not normally distributed.

Parametric multivariate analyses are much more sensitive to data not meeting their required assumptions of homogeneous within-group covariance matrices and

multivariate normal data distributions than univariate analyses. However, the main parameters affected by deviations from assumptions are the significance of results. Therefore, failure of one or more assumptions does not make a procedure like discriminant analysis futile, but one should be cautious when interpreting the significance of the results (Manley 1986, p.90). Again, hence the use of the smaller significance level of 0.01.

5.3 Species sub-groups

Table 5.1 Species groups (or individuals for size-classes) for woody-species analyses.

Life-form:	Large-tree species	Species whose adult heights are normally > 20 m
	Medium-tree species	Species whose adult heights are normally 10-20 m
	Small-tree species	Species whose adult heights are normally 3-10 m
	Shrub species	Species whose adult heights are normally < 3 m
Seed-mass:	Group 1	Species with mean, dried seed mass > 1.0 g
	Group 2	Species with mean, dried seed mass 0.1-1.0 g
	Group 3	Species with mean, dried seed mass 0.001-0.1 g[11]
	Group 4	Species with mean dried-seed mass < 0.001 g.
	Other	Seed-mass unknown or species vegetative only
Size-class:	Small seedlings	Individuals ≤ 25 cm height
	Seedlings	Individuals ≤ 100 cm height but > 25 cm
	Large seedlings/small saplings	Individuals >100 cm height and < 1 cm diameter
	Saplings	Individuals with heights 1-4 m but diameter ≥ 1 cm[12]
	Large saplings/small trees	Individuals with heights 4-10 m, diameters > 1 cm
	Medium trees	Individuals with heights 10-20 m
	Large trees	Individuals with heights > 20 m

In some analyses, plants were sub-grouped into species-groups or size classes to find patterns in the data. For non-woody species, species groups used in the analyses were based on life-forms: ferns, herbs, grasses, and lianas. Tree and shrub (woody) species were sub-grouped by seed-mass, life-forms (Table 5.1; Appendix B

[11] Two groups were joined together here because there were so few species with mass 0.001-0.01 g.
[12] Monocots *Clinostigma* and *Pandanas*, and *Cyathea* tree-fern were quite abundant in the plots but their growth patterns and leaf/frond sizes meant that I thought they should be treated differently from the woody dicot species. Consequently, for the sapling size class, the diameter ruling was removed and instead required only that heights be ≥1.5 m and ≤ 4 m. Other classes were unaffected because all individual monocots with heights > 4 m had measurable diameters.

for seed-mass and life-form characteristics of species), or common individual species; individuals were sometimes sub-grouped by size-classes (Table 5.1).

5.4 Statistical procedures for comparing plot types at time 0 and over 15 months

5.4.1 Analysis of frequencies

Frequency records in this study were of three types: new recruitment (individuals arriving after time 0), mortality, and overall standing-stock at a particular time. Tree and shrub stem frequencies were compared between or among plot types, overall or sub-grouped by life-form, seed-mass, size-class, or common individual species; and over time. Graph and table frequencies are comparable because they were standardised first to an equal area of 100 quadrats per plot type (see standardisation section 5.1). The statistical procedures used to analyse the frequencies alone were G-tests, log-linear modelling, and correspondence analysis.

G-test/likelihood ratio chi-square

Plot type comparisons at time 0 were analysed using standardised frequency data with G-tests. The G-test, also known as the log-likelihood ratio test, is a similar statistical test to chi-square. It tests the goodness of fit between observed and expected frequencies for single-classification data, for example, total frequencies among the three plot types or the independence/no association of frequencies within an r x c contingency table. The G-test is distributed as approximately chi-square and has the formula:

$G=2\Sigma^{a} fi \ln(fi/f\hat{}i)$

where a is the number of classes, fi is the observed frequency, and $f\hat{}i$ is the expected frequency (Sokal & Rohlf 1995, p.699). In SAS, it is computed as one of the chi-square tests ("likelihood ratio chi-square") in PROC FREQ.

Frequencies in a contingency table were grouped by plot type (column variables) and either totals only (i.e., no row variables) or a species sub-group such as

life-form for the row variables. In the latter, an r x c table, the G-test examined whether there was any association between the plot types and life-forms.

Where test statistics were marginally significant, the Williams correction factor was applied to help the distribution more closely approximate the chi-square by reducing the observed value of G slightly. The Williams correction factor for an r x c table is:

$$q=1+\{(n^{b}\Sigma\ 1/\Sigma fi-1)(n^{a}\Sigma\ 1/\Sigma fi-1)\}/\{6n(a-1)(b-1)\}$$

where a is the number of column classes, b is the number of row classes, *f*i is the observed frequency, and n is the total frequency (Sokal & Rohlf 1995, p.738). For a simple goodness-of-fit test for single-classification data, it is: $q=1+\{(a^2-1)/6n(a-1)\}$ (ibid., p.699).

Log-linear modelling

A major aspect of testing the frequencies from each plot type was that after the first census, there were three data dimensions: plot type, species-group such as life-form, seed-mass or common species individually; and time. These were presented as three-way contingency tables and the data were tested for patterns among the variables, with particular interest not on main effects but on the interactions, for example, an interaction between plot type and time. For this I used log-linear modelling (PROC CATMOD in SAS).

Log-linear modelling is to categorical data what analysis of variance and multiple regression are to continuous variables (Sokal & Rohlf 1995, p.744). The null hypothesis is that all variables are independent of (or unassociated with) each other, much like the G-test for independence in a two-way table. For a three-way contingency table the log-linear model is:

$$\text{Ln } f_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$$

where f_{ijk} is the expected frequency for row i, column j, and depth k; μ is the mean of the logarithms of the expected frequencies; $\alpha_i + \beta_j + \gamma_k$ are the main effects of categories i, j, and k of factors A, B, and C, respectively; $\alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk}$ are the second-order interaction effects of the dependence of each category of a factor on the category of one of the other two factors; and $\alpha\beta\gamma_{ijk}$ is the third-order interaction between all combinations of all categories and factors (ibid., p.744).

Raw frequencies were used in the time-series analyses with CATMOD because the procedure tolerates unequal sample sizes for interactions, and the interest with time-series lay in the interactions rather than main effects. Four census times were used in the analyses although the one-month time had no data for SAF.

Correspondence analysis

In SAS, Correspondence analysis (CA) graphically shows the main patterns in a contingency table, such as any associations among plot types and among life-forms on the same graph. It is a weighted principle components analysis that finds a low dimensional representation of the association between rows and columns of a table through comparing expected and observed frequencies similar to the process of chi-square tests. I used PROC CORRESP in SAS.

There are two main biases in CA (Ter Braak 1995):

1) The "arch" effect, where the second axis (and any subsequent ones) introduces an arch shape into the first because of a systematic (often quadratic) relationship between the axes. This causes differences along the second axis to appear greater than they truly are.
2) Points at the ends of the axes are often compressed relative to the middle.

CA is not usually recommended for data sets that have more than one important axis of variation. In all analyses where I used CA in this thesis, however, the first axis always accounted for the vast majority of the variation among species or species sub-groups, and plot types. Therefore, if the second axis is not needed for interpretation, the main problem with CA is avoided. Ludwig and Reynolds (1988) suggest that CA performs well when dealing with community data with one dominant gradient covering a broad environmental gradient, but that de-trended correspondence analysis should also be done when an arch is evident in the CA.

5.4.2 Height and diameter growth

Mean absolute and proportional height growth were analysed for plants that were present at time 0 and survived to 15 months. Height growth 3-15 months was analysed for all plants present at both three and 15 months to compare growth among recruitment cohorts (time 0 cohort vs. new recruits). Mean net height over time was also analysed. Death of an individual produced a negative height change and a new

recruit gave a positive height change. Results were very similar for the two methods, but survivors' height growth data highlighted trends and distinctions more clearly and better served my analysis needs.

Mean absolute height growth[13] was merely the plot (or quadrat) mean of plant height at time t_{n+1} minus plant height at t_n. Mean proportional height growth (no unit) was:

(plant height at t_{n+1} - plant height at t_n)/plant height at t_n.

The proportional growth rate was used to reduce the effect of different initial plant heights (similar to taking logarithms of plant heights). It was used rather than a relative growth rate, RGR (sensu Hunt 1982), because the census periods were the same for all surviving plants (i.e., a constant denominator for RGR). Conclusions from significance tests were almost always the same for absolute and proportional height growth, but proportional growth results usually highlighted differences better and so were more commonly presented.

Analysis of diameter growth used survivors only to remove trees felled in gap plots. However, survival of trees large enough for diameter measurements was high so there was little difference between survivors' growth and net growth. There were no height restrictions. Diameter growth was not sub-grouped by size-class, seed-group or life-form because the number of missing values was too large for seed groups 3 and 4, and because shrubs and small-tree species, though numerous, were rarely large enough to have dbh ≥ 1 cm.

Analysis of variance (ANOVA), repeated-measures ANOVA

ANOVA models (with PROC GLM in SAS) were used to test whether mean plot- (and quadrat-) height growth between 0 and 15 months was different among the three plot types. Diameter growth was also modelled. When significant differences were found among the plot types at $p<0.01$, a Fisher's LSD test was used to see which plot type mean(s) was significantly different from the others (MEANS option in PROC GLM). Of the commonly used multiple comparison tests, the Fisher's LSD is among the most sensitive: the probability of falsely finding a pair of means to be different is

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[13] Data sets for height growth tests excluded individuals > 10 m height because over 15 months height growth of large trees was minimal compared to the level of measurement error, but these measurement changes (e.g., plus or minus 0.5-2 metres) would have had a disproportionately large influence on results.

higher with LSD than, say, Tukey (one of the most conservative tests). Conversely, the probability of falsely declaring no differences between means when in fact there really are is higher for Tukey than LSD. In practice, the prescribed significance level, here, p=0.01 rather than 0.05, made more difference in whether means were declared significantly different than which particular comparison test was used. Both LSD and Tukey tests were routinely tested and declarations were identical in most cases. When they differed, LSD results were applied because it was felt that Tukey tests were unnecessarily (and perhaps, misleadingly) conservative when using the prescribed 0.01 significance level.

Repeated-measures ANOVA was used to test growth over each time period (0, 3, and 15 months). Repeated-measures ANOVA is a special case of multiple ANOVA (MANOVA). Hypothesis testing focuses on between-subject effects, which are the experimental factors, for example, plot type; within-subject effects, which are effects due to the repeated measurements such as time; and the interaction between these two effects. Tests were carried out in SAS using PROC GLM with a 'repeated' statement and appropriate contrasts.

(canonical) Discriminant analysis

Discriminant Analysis (DA) tries to maximise differences between known groups that have been measured for several variables. In this thesis, DA was used to test whether plot types could be better separated by including data sub-grouped by life-form, seed-group, size-class, or common individual species, treating each sub-group as a variable. An analysis with no species sub-groups but using several of the measured variables (e.g., height growth, non-woody cover, new recruit frequencies) to separate the plot types, was also run. In SAS, I used PROC DISCRIM.

The number of missing values in sub-groups precluded diameter growth with species sub-groups being used in DA. The lighter seed-mass groups (3 and 4) did not have large enough numbers present in MPF or GPF. Also, the life-forms shrubs and small-tree species were rarely large enough to have diameters at 1.3 m of at least 1 cm.

Linear rather than quadratic discriminant functions were used with the plot data because with only 18 sample units, the reliability of any homogeneity-of-variance tests (Bartlett's test in DISCRIM) was not assured. Linear discriminant functions provided

more conservative results and helped buffer against over-sensitive interpretations caused by weak fitting normality or homogeneous-variance test assumptions. Eigenvalues and coefficients remain invariant under quadratic and linear functions; only substitutions and Mahalanobis distances change. The signs and relative magnitudes of the intra-set correlations and standardised canonical coefficients help show the relative importance of each variable or species group in separating plot types (Manley 1986).

5.4.3 Micro-environmental variables and their changes through time

Micro-environmental variables canopy openness, litter cover, and litter depth were individually analysed (after arc-sine transformations for the percentages) with ANOVA to test whether there were differences among plot types. The variables were also analysed at time 0, together with area-coverage by rocks and roots, for overall plot type micro-environmental differences using multiple ANOVA ('manova' option in PROC GLM in SAS). Repeated-measures ANOVA then tested for differences over the three main censuses, or the first two censuses for litter cover. Quadrat light measurements from the three methods used in the study - canopy openness, hemispherical photographs, and light-sensitive papers – were compared using Spearman's correlation.

5.4.4 Non-woody cover and epiphytes

Area-coverage data for lianas, ferns, grasses and herbs rooted in the ground (non-woody cover), and epiphytes found on recorded trees, were all transformed by arc-sine then analysed with ANOVA to test whether plot types differed in these response variables at time 0. Mean percent non-woody cover was also tested with repeated-measures ANOVA for differences among the plot types 0-15 months.

5.4.5 Health

G tests were used to compare tree and shrub health among plot types and species groups. Analyses tested for associations among plot type and species groups in

the proportion of healthy vs. non-healthy individuals at time 0 and at 3 months, and among non-health codes. Non-health codes were grouped as:

- **Biotic:** those damaged by insects, fungal pathogens, or covered by lichens and mosses, and covering more than half of the plant's leaf area (field codes 02, 03, 04, 09, 10, moderate to heavy cover only).
- **Physically damaged – bent**: physically damaged, and bent more than 45 degrees (field code 05, moderate to heavy damage only).
- **Physically damaged – not bent**: largely branch damage or a broken central leader (field codes 06, 07, 08, moderately to heavily damaged plants only).
- **Drought-stressed**: drought stressed, wilting or singed leaves, die-back, moderately or strongly affecting the plant (field code 14).

5.5 Relationships amongst micro-environmental and biotic variables

Non-parametric Spearman's rank correlations

Spearman's rank correlations (PROC CORR in SAS) were used to test for associations between pairs of quadrat-level variables; for example, canopy openness vs. height growth, non-woody cover, or axes derived from DCA ordinations. Rather than testing the association between measured data from two variables, the data are first ranked and then the ranks are tested for association. The null hypothesis is that there is near-zero rank correlation between two variables, X and Y, provided that X and Y have independent distributions and observations were randomly sampled (Sprent 1989, p.136). Spearman's correlation was used rather than the parametric Pearson correlation because quadrat data were non-normal.

De-trended correspondence analysis (DCA)

DCA (in PC-ORD Multivariate Analysis of Ecological Data, Version 3.0 for Windows, by MjM Software Design, 1997) was used to explore spatial patterns of species presence among quadrats. Ordination axes were then tested against quadrat-level micro-environmental variables using Spearman's correlations (see above). DCA is an indirect ordination technique that is similar to Correspondence Analysis (CA) but

is often more appropriate than CA for exploring complex, potentially non-linear, ecological data. DCA is most commonly used to explore spatial patterns in species presence or abundance, as it was here. Ordinations maximise the variation among species based on gradients of other (usually environmental) variables such as light, slope, or aspect of sample sites. In DCA, data are de-trended to remove any arch shape caused by a relationship between the first and second ordination axes, as can occur in CA; the axes are also re-scaled to smooth the within-sample variance of species scores along the ordination axis (McCune & Mefford 1995).

Canonical correlation analysis

Canonical correlation analysis (CCA) was used to investigate the main relationships between micro-environmental factors and plant variables. CCA solves by looking for linear combinations of two sets of variables that are highly correlated. The correlation between two sets is found while adjusting for within-set correlations. Each new pair of variables represents an independent dimension of the relationship between the two sets of variables, with the first pair having the largest possible correlation so being the most important. Looking at the coefficients making up each pair of canonical variables helps explain the main sources of similarity (or dissimilarity) between the two sets of original variables. CCA is related to DA but the emphasis is on comparing sets of variables rather than sets of individuals. Micro-environmental variables analysed at time 0 were canopy openness, litter volume, debris cover, and rock cover. Biotic variables analysed were tree (and shrub) frequencies, mean height, and mean area covered by non-woody species.

Regression analysis

Simple linear regression analysis was used to examine whether plot-level light (and litter depth for new recruits) affected plant responses. In particular, I tested the hypotheses that light causally affected total stem frequencies, the abundance of new recruits, plant height growth, and coverage of non-woody species; also whether non-woody cover caused an effect in the frequency of new recruits. Tests used PROC REG or PROC GLM in SAS.

Results

Chapter Six: Forests at Time 0

A preliminary survey of the disturbance regime in Pohnpei's upland forest provides a backdrop to the time 0 census by illustrating natural scales of change in the forest as opposed to disturbance induced when forest is converted to sakau cultivation. At time 0, plots classed as mature-phase forest (MPF) were assumed to be practically the same as plots that changed from mature-phase to gap-phase forest (GPF) after tree felling. MPF and GPF census data were assessed to test this assumption. Once satisfied with the validity of this assumption, the forest plot-type data were pooled (MPFpooled) and compared to sakau-agro-forest (SAF).

6.1 Natural forest disturbance

In the preliminary forest survey, 192 disturbances from large-branch falls to multiple tree-falls were recorded from 14 transects (transect area totalled two hectares: 2000 m in length by 10 m width). Overall, the larger the disturbance, the more rarely it occurred (Figures 6.1 and 6.2). Conversely, smaller disturbances were far more frequent.

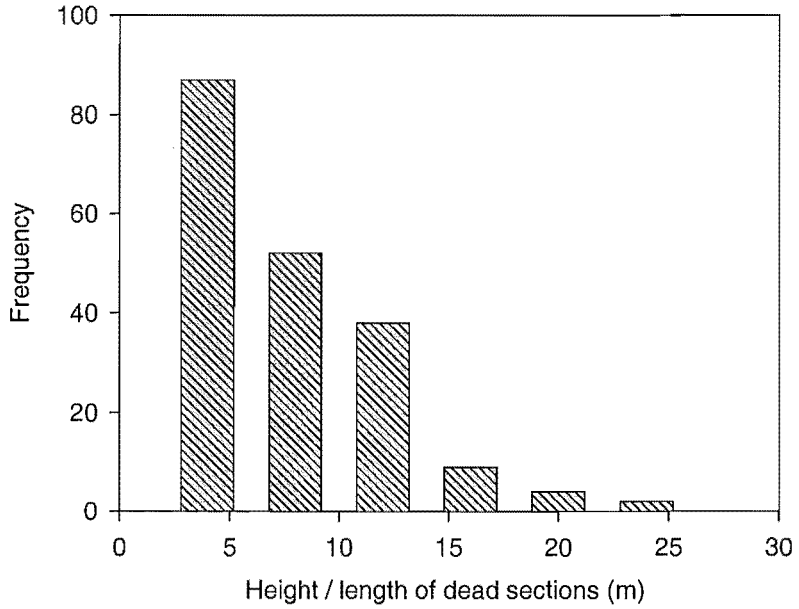


Figure 6.1 Height/length distribution of disturbance creators.
Heights were recorded for standing-dead trees, and lengths for fallen trees (or parts of trees). Heights or lengths were only for the dead sections of trees (i.e., residual live parts of trees for branch-falls, were excluded).

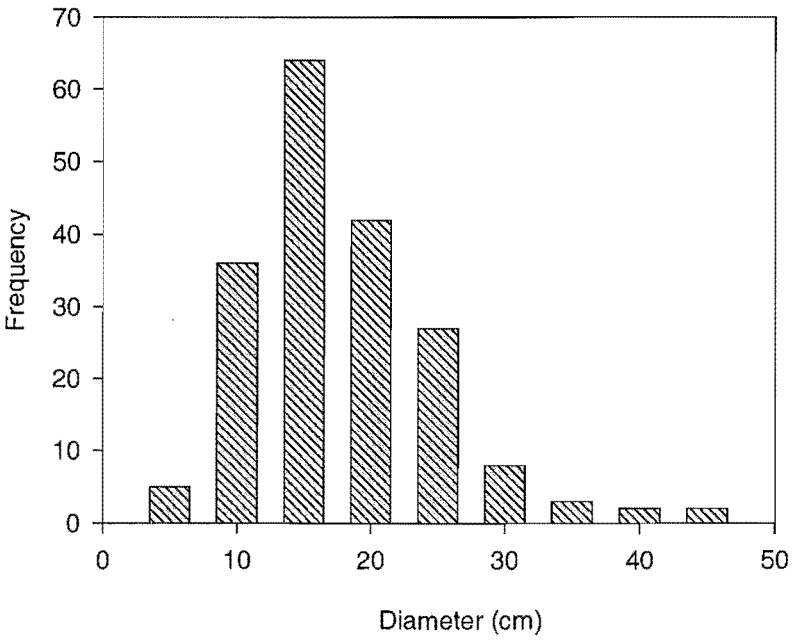


Figure 6.2 Diameter distribution of disturbance creators.
Diameters were only for the dead sections of trees (i.e., residual live parts of trees for branch-falls were excluded), and were taken where practicable at 1.3 m height.

Table 6.1 Notes for each disturbance type.
Diameters and heights/lengths are for the dead sections of trees only (i.e., residual live parts of trees were excluded).

Individual tree/branch disturbance:	Relative frequency (% of total disturbances) [frequencies in brackets]	Mean length (m) of dead section	Mean diameter (cm) of dead section	Most common disturbing species
Fallen branch	8 % [15]	4.42	16.24	*Campnosperma*
Sub-canopy tree fall	68 % [131]	4.44	14.43	*Cyathea*
Standing-dead tree	7 % [13]	6.49	13.31	*Parinari*
Uprooted/wind-thrown tree	11 % [22]	10.93	26.54	*Campnosperma*, *Clinostigma*
Blown tops/ snapped tree	6 % [11]	11.9	29.35	All large-tree species, (e.g., *Clinostigma* *Campnosperma*, , *Myristica*)

On an individual-tree/branch level (Table 6.1), branch-falls and sub-canopy (mostly *Cyathea*) tree-falls were the smallest and most common disturbers, and uprooted trees and snapped trees the largest. Most trees or branches were found either alone or with one or two others. However, there were two disturbances where more than three trees had died together: one area had several small *Parinari* standing dead alongside fallen *Parinari* and *Clinostigma*, and another had several large fallen *Parinari* and *Myristica*.

Small-scale disturbance is indeed very frequent in the upland forest, almost continuous. *Clinostigma* fronds falling from the palm tops some 20-35 m above the forest floor can be heard continually. Seedling health data (see, for example, time 0 health, Tables 6.2, 6.11) show that many seedlings are bent or covered by debris in closed forest, most commonly from *Clinostigma* fronds. They also appear to be quite adapted to re-sprouting after small disturbances, especially *Parinari*, and *Aglaia ponapensis* Kaneh., which can re-sprout from a cut pole. Such disturbances are very localised in their impact (i.e., usually less than a one-metre-square area) and therefore affect the relative competitive hierachy among plants within only that localised area. This, plus branch-falls from large standing-dead or live canopy trees and mid-canopy small-tree and *Cyathea* falls create a closed "undisturbed" forest that has constant low-level disturbance throughout.

Standing dead trees produce small-to-medium-sized disturbances as the tree gradually disintegrates. On average, standing dead trees were greater in height than the branch-falls and *Cyathea* falls but diameters were similar. *Parinari* often dies standing. Pathogenic infection was observed to be associated with standing death for *Parinari* trees as well as other mid-canopy trees like *Garcinia ponapensis* Lauterb.. Several trees were sometimes infected in one area, probably increasing the gap size over time.

Uprooted trees were higher in average height and diameter than the above disturbance types. Only snapped trees were larger. In the survey, *Clinostigma* palms were the most numerous of the uprooted trees. Yet the area disturbed when a *Clinostigma* falls is quite small because of their thin boles, absence of branches and frond mass only at the top of the palm. Other species found uprooted included *Campnosperma, Hibiscus tiliaceus* L., *Myristica*, and *Palaqium.*

Large hardwood tree falls were the least numerous, but they created the largest individual canopy openings. Typically, the largest individuals of the canopy species, *Campnosperma, Clinostigma, Myristica, Elaeocarpus carolinensis* Koidz., and *Parinari*, snap 1-8 m above the base of the stem. Of these, the full crown and branching mass of large *Myristica* and to a lesser extent *Parinari* produce the largest single-tree disturbances. *Clinostigma*, although co-dominant with *Campnosperma*, does not produce a large gap because of its thin bole and absence of branches. *Elaeocarpus* and *Campnosperma* also produce large single-tree falls although their branching habits are sparse compared to *Myristica* and *Parinari.*

The recorded rate of disturbances has most likely been affected by the decomposition rates (at present not quantitatively known) of the different species. *Cyathea* appeared to decompose very slowly compared to other species because of its very dense and fibrous stem and roots. In contrast, the soft palm stem and fronds of *Clinostigma* may predispose it to rapid decomposition. *Elaeocarpus* and *Myristica* both have very dense woods and remain on the ground considerably longer than *Clinostigma*, and probably also *Campnosperma.* The large numbers for *Cyathea* disturbances, therefore, may relate to the stems remaining intact for longer on the ground than the tree species, over-estimating their predominance, while *Clinostigma* and maybe *Campnosperma* numbers are probably under-recorded compared to their presence in the forest. Also, the rapid decomposition of some trees and the shattering of tree trunks on ground impact made measuring tree lengths quite ambiguous.

Recorded tree lengths for the uprooted and snapped trees, therefore, are likely to be underestimated. Hence, when we examine the overall height/length and diameter distributions (Figures 6.1 and 6.2, respectively), they are highly skewed by the *Cyathea* data and short fallen-tree lengths towards the low end of the size distributions. Nevertheless, even if the *Cyathea* numbers are overestimated and species like *Clinostigma* underestimated, the trend would be similar, but less dominated by *Cyathea.*

Single-to-few-tree falls were chosen as the experimental forest-gap makers. Due to the prevalence of almost continuous very small disturbances, a gap-size was needed that would allow environmental changes and changes to plant growth in this broad-scale ecological sampling to be apparent. Single-tree falls represent the mid-point between large-scale, rare, many-tree-fall gaps and the highly frequent small disturbances. Primarily, one large tree was felled to create gaps. However, usually one or two other smaller trees were knocked over by (but in the same direction as) the main falling tree.

Disturbances created from a medium-to-large (40-60 cm) *Campnosperma, Parinari, Myristica, or Elaeocarpus* were used for several reasons. Hardwoods were used instead of *Clinostigma* because although the *Clinostigma* palm-falls were the most common whole-tree falls, the disturbances created would have been too small to allow the detection of any changes with the quadrats laid out on a 15-m radius. Perhaps a radius of 12 m or even 10 m would have been more desirable for detecting smaller-scale disturbances but the 15-m radius was better for sampling the full range of conditions in sakau plots. Also, large hardwoods disturb a considerably greater area when they do fall, so arguably it is they that change conditions for regeneration in the understorey.

6.2 Plot types at time 0

6.2.1 Forest plots

At the initial census, fourteen mature-phase forest plots were established. After being censused, they were randomly allocated to either the "mature-phase forest" (MPF) plot type or to "gap-phase forest" (GPF). The latter were mature-phase at the time 0 census but then became "gap-phase" through tree falls. The following results compare the initial characteristics of the plots grouped as "mature-phase forest" with those grouped as "gap-phase forest". This tested whether they were indeed equivalent at time 0 before the gaps were created, and provided a scale of natural variation within mature forest against which to consider the gap-mature forest contrast. Variation between plot-types (derived from the grouped plot means) and among plots (derived from the grouped quadrat means within each plot) was examined.

Between plot-types

At the prescribed significance level, α, of 0.01, no significant differences existed between MPF and GPF at time 0 for the micro-environmental variables measured, nor for species richness, total stem frequencies, mean stem height, mean stem diameter, seedling health, non-woody species coverage or epiphyte coverage (all species combined) (Table 6.2). No significant differences were found at time 0 between the two plot types for the number of quadrats in which a life-form or species occurred (Figures 6.3 and 6.4, respectively).

Table 6.2. A summary of comparisons at time 0 between MPF and plots that became GPF after time 0.

MICRO-ENVIRONMENT CHARACTERISTICS:	**Mature-phase forest**	**Gap-phase forest**	**Statistical tests-MPF vs GPF**
Mean canopy openness (%) ± s.e.	4.70 ± 0.31	5.26 ± 0.44	F =1.11, p=0.3143
Direct site factor (dsfc) (%) ± s.e.	3.81 ± 0.09 (n=2)	5.78 ± 2.0 (n=2)	F=0.92, p=0.4390
Indirect site factor (isfc) (%) ± s.e.	2.67 ± 0.00 (n=2)	3.91 ± 0.7 (n=2)	F=2.79, p=0.2365
Mean leaf litter cover (%) ± s.e.	70.77 ± 4.43	69.54 ± 5.84	F =0.02, p=0.8867
Mean litter depth (cm) ± s.e.	1.89 ± 0.13	2.15 ± 0.07	F =2.96, p=0.1136
Mean debris cover (%) ± s.e	3.13 ± 0.63	0.80 ± 0.20	F=5.50, p=0.0388
Mean coverage of rocks & roots (%) ± s.e.	16.82 ± 5.37	18.72 ± 6.72	F=0.05, p=0.8813
PLANT CHARACTERISTICS:	**Mature-phase forest**	**Gap-phase forest**	**Statistical tests- MPF vs. GPF**
Species richness (no. spp. present)			
Life-form:			
Trees and shrubs	26	20	G (plot type x spp. richness) =1.45, p=0.693;
Lianas	9	9	
Herbs and grasses	6	6	
Ferns	16	21	
Total	57	56	
TREES AND SHRUBS			
Stem frequencies summed per plot type [in brackets: per m^2 ± s.e.]			
All individuals combined:	1428 [13.26 ± 1.01]	1428[13.52 ± 0.98]	G=0.00, p=1.00
By Life-form:			
Large tree spp.	1029 [9.62 ± 1.36]	1040 [9.97 ± 1.28]	G (plot-type x life-form) =8.89, p=0.031
Medium tree spp.	65 [0.60 ± 0.17]	41 [0.38 ± 0.18]	
Small tree spp.	297 [2.70 ± 0.71]	322 [2.92 ± 0.73]	
Shrub spp.	37 [0.34 ± 0.19]	25 [0.26 ± 0.10]	
By Seed-mass group:			
1 (x ≥ 1.0 g)	788 [7.34 ± 1.37]	656 [6.30 ± 0.95]	G (plot-type x seed-mass group) =35.09, p=0.001
2 (0.1 g ≤ x < 1.0 g)	526 [4.87 ± 1.11]	665 [6.21 ± 0.81]	
3 (0.001 g ≤ x < 0.1 g)	72 [0.67 ± 0.10]	84 [0.83 ± 0.20]	
4 (x < 0.001 g)	41 [0.36 ± 0.11]	22 [0.17 ± 0.07]	
By Size-class:			
Small seedlings	510 [5.09 ± 1.05]	650 [6.53 ± 0.71]	G (plot-type x size-class)[1] =36.79, p=0.001 [1]medium and large trees were combined for G test. [2] large saplings, medium trees, and large trees were combined for freq/m^2 calculation.
Seedlings	636 [6.36 ± 1.02]	568 [5.63 ± 0.73	
Large seedlings	111 [1.10 ± 0.34]	75 [0.73 ± 0.20]	
Saplings	108 [0.27 ± 0.04]	87 [0.22 ± 0.04]	
Large saplings	36 [0.16 ± 0.02] [2]	18 [0.12 ± 0.02]	
Medium trees	17	15	
Large trees	9	17	
Mean height (m) ± s.e.	1.12 ± 0.06	1.06 ± 0.07	F=0.54, p=0.4794
Mean diameter at 1.3 m (cm)± s.e.	7.21 ± 1.10	10.80 ± 1.79	F =2.96, p=0.1134
Health (seedlings ≤ 1.0 m hgt.):			
% healthy [#]	73.45 % [842/1146]	70.65 % [860/1217]	G (plot-type x healthy vs. not healthy) =2.95, p=0.086; G (plot-type x 3 non-health codes) =7.04, p=0.030;
% physical damage & bent [#]	16.37 % [188]	18.65 % [227]	
% physical damage – not bent [#]	3.16 % [36]	4.70 % [57]	
% biotic coverage [#]	7.02 % [80]	5.73 % [70]	
Ferns, grasses, herbs, lianas:			
Mean % cover/m^2 ± s.e.	2.31 ± 0.82	2.23 ±0.65	F=0.02, p=0.8868
% quadrats with non-woody spp.	77 %	79 %	
Epiphytes:			
Mean % cover/tree± s.e.	6.69 ± 1.27	5.02 ± 0.83	F=1.13, p=0.3105
% quadrats with epiphytes	42 %	50 %	

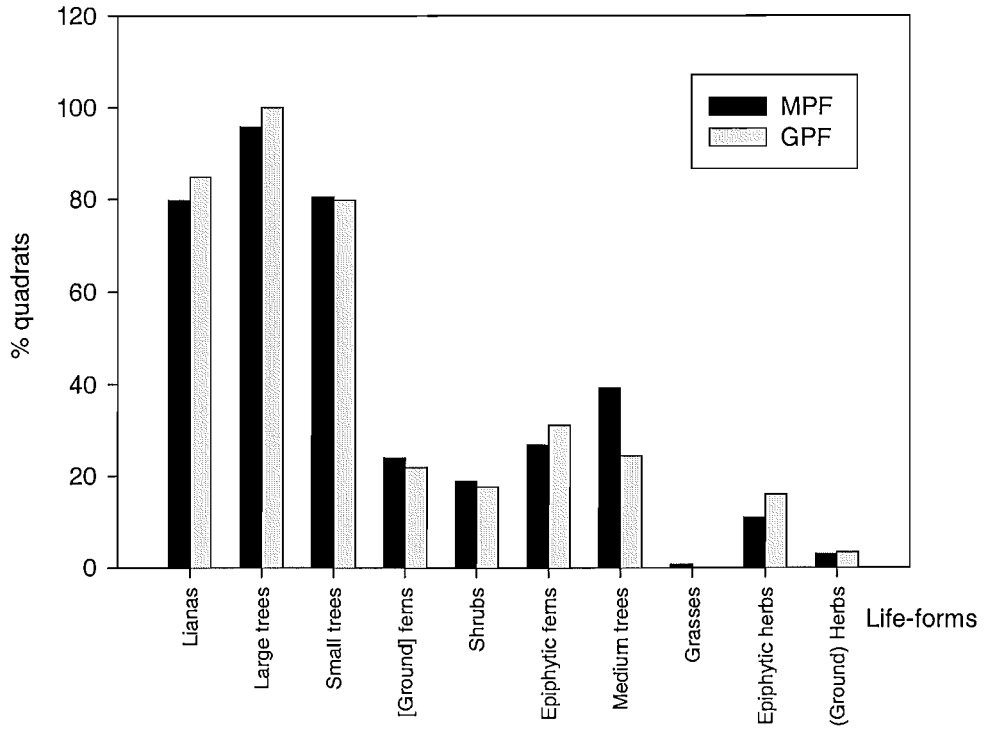


Figure 6.3 Presence of life-forms in MPF and GPF at time 0.
Presence is the percentage of quadrats per plot type in which each species occurred.

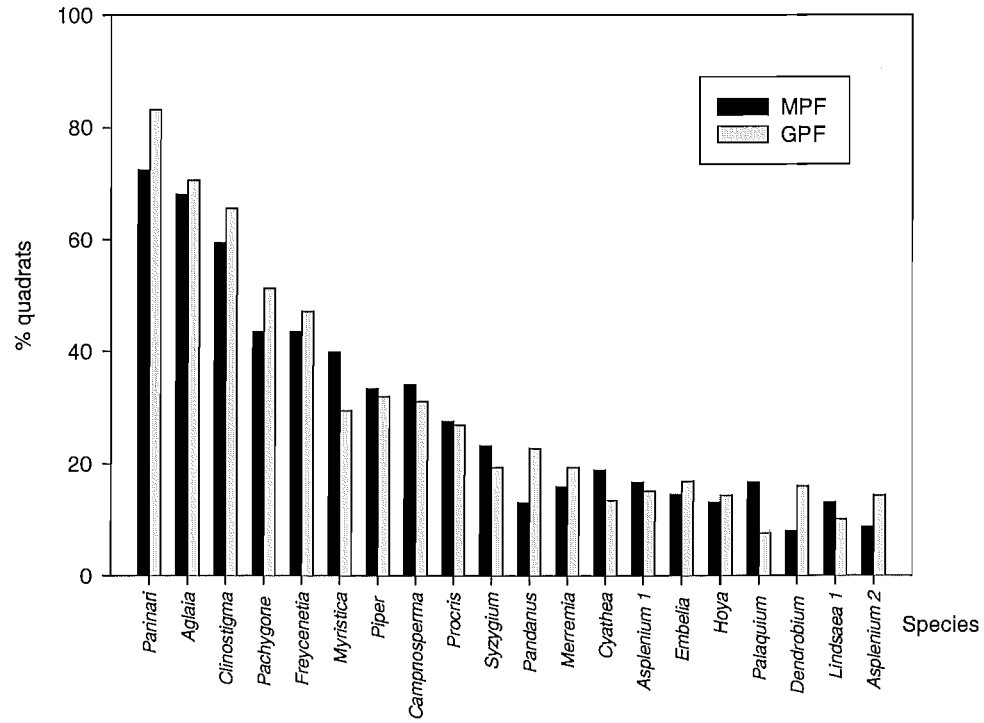


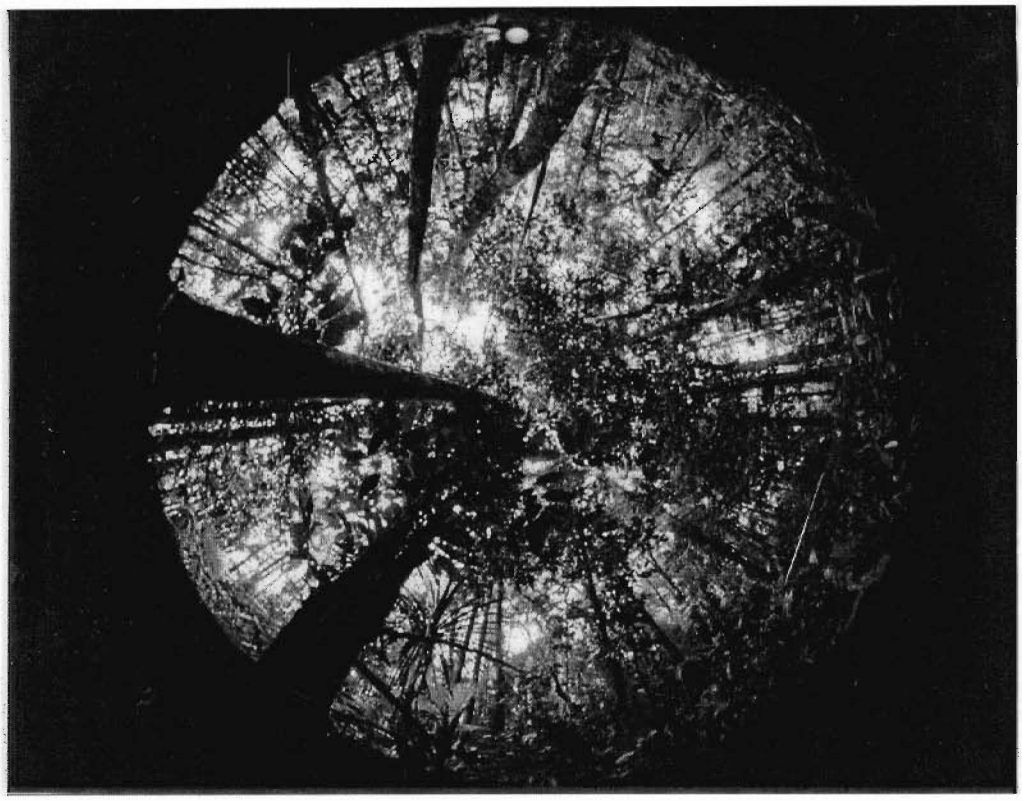
Figure 6.4 Presence of the 20 most common species in MPF and GPF at time 0.
Presence is the percentage of quadrats per plot type in which each species occurred.

Overall, the total stem frequencies in each plot type, 1428 (standardised to 100 quadrats), were equal. However, there were significant interactions between the plot-types and both seed-mass groups and size-classes (Table 6.2). G-tests for individual species frequencies indicated that *Clinostigma* was present in significantly greater frequencies in GPF (329 in total) than MPF (203) at time 0. Conversely, *Myristica* and *Parinari* were in significantly greater frequencies in MPF (105 and 675, respectively) than in GPF (65 and 587) (see Appendix C for stem frequencies over time for individual species). These species differences help to explain the significant plot type by seed-mass and size-class results: *Clinostigma* is classed in seed-mass group 2 and its juveniles are generally small seedlings (less than 25 cm height), while *Parinari* is classed in seed-mass group 1 and juveniles are usually classed as seedlings (25-100 cm). Hence, GPF had more individuals in small-seedling and seed-group 2 classes, and MPF had greater representation from seedlings and seed-group 1.

As both plot types are theoretically (and overall, statistically) the same at time 0, the frequency differences for *Clinostigma*, *Myristica*, and *Parinari* represent the patchy occurrence of these species. Notably, *Parinari* and *Myristica* have large fruits. *Myristica* may be dispersed by *mwuroi*/Micronesian pigeon (*Ducula oceanica*), but *Parinari* appears to have no animal disperser for its fruits on Pohnpei and therefore relies solely on gravity (barochory), the fruits merely dropping to the ground and seeds germinating near the parent.

Among plots

No significant differences were found among individual plots (using quadrat-means) for mean height ($F=1.12$, $p=0.3458$) or mean diameter ($F=1.61$, $p=0.0898$). However, there were significant differences among plots for all micro-environmental variables (all variables had $p=0.0001$ except woody debris which was insignificant ($p=0.1411$)), and for area-coverage by non-woody species ($F=3.03$, $p=0.0005$). The differences among plots reflect inherent forest variability (for example, Figures 6.5a,b). Some sites were steep, others flat, some were more rocky than others (see Table 4.1 in methods section). Controlling for slope was impossible in practice so forest areas were chosen to cover the range of site conditions. However, differences between the plots were not very definite (e.g., LSD results for canopy openness, which had the widest range in results, Table 6.3).



a)

b)

Figure 6.5 Variation in canopy openness among forest plots at time 0 as seen by hemispherical photographs.
a) one of the darkest quadrats (ISFC=0.013, canopy openness =4.42 %), b) one of the lightest quadrats (ISFC=0.079, canopy openness = 8.84 %).

Table 6.3: LSD multiple comparisons for canopy openness.
Means with the same letter are not significantly different at α=0.01.

plot	15	14	17	6	7	16	13	9	12	10	8	11	18
canopy openness (%)	6.91 ±0.68	5.98 ±0.51	5.86 ±0.28	5.45 ±0.29	5.37 ±0.22	4.97 ±0.26	4.98 ±0.37	4.68 ±0.28	4.63 ±0.29	4.15 ±0.29	3.98 ±0.28	3.76 ±0.13	3.71 ±0.17
LSD groupings	a	ab	ab	bc	bc	bcd	bcd	cde	cde	de	de	e	e

6.2.2 Sakau plots

No significant differences occurred among the five sakau plots for leaf litter cover, litter depth, or non-woody cover. However, there were significant differences among plots for mean stem height (F=4.25, p=0.0035), mean stem diameter (F=3.61, p=0.0140), and area-coverage by rocks and roots (F=3.24, p=0.0154); canopy openness was marginally significant (F=2.95, p=0.0240). The multiple ANOVA (MANOVA) result for all micro-environmental factors was significant (F=2.05, p=0.0105). Thus, inherent variability was high. The highly heterogeneous nature of the vegetation is why 0.01 rather than 0.05 was used as the main significance level for comparisons. Even so, the sakau plots were particularly variable because the quadrats ranged from plot centres that were very open to edges with more intact forest (e.g., Figures 6.6a, b), plus a few, remnant forest trees remained within some plots.

a)

b)

Figure 6.6 Variation in canopy openness among sakau plots at time 0 as seen by hemispherical photographs.

a) one of the darkest quadrats (ISFC=0.025, canopy openness=7.54 %), b) one of the lightest quadrats (ISFC=0.535, canopy openness=56.94 %).

6.2.3 Mature-phase forest vs. sakau agro-forest

Note that for frequency variables at time 0, MPF and GPF plots were pooled for graphs and tables, and all plot types were standardised to 100 quadrats. However, for statistical analyses with plot means, the two mature-phase forest plot types (MPF and GPF) were separated so as not to unbalance plot numbers too greatly in the ANOVA tests (i.e., seven and seven vs. five plots instead of 14 vs. five), but the results are presented with the forest plots pooled.

Micro-environment

The micro-environments of MPF and SAF were significantly different at time 0 (Table 6.4).

Table 6.4 Micro-environmental characteristics of MPF_{pooled} and SAF at time 0.
Note: for photo-papers, the data came from two of the seven MPF plots only and none from GPF.

	Mature-phase forest	Sakau-agro forest	Statistical tests
Mean canopy openness (%) ± s.e.	4.96 ± 0.26	24.61 ± 2.67	F =86.11, p=0.0001
DSFC (%)± s.e. (n=4,2)	4.80 ± 1.0	29.72 ± 2.1	F=71.36, p=0.0030
ISFC (%)± s.e. (n=4,2)	3.29 ± 0.5	21.90 ± 3.1	F=34.49, p=0.0085
Photo-papers 1 m (n=39 quadrats)	3.41 ± 0.10	4.93 ± 0.18	F=56.41, p=0.0001
Photo-papers 3 m (n=38 quadrats)	3.41 ± 0.12	5.38 ± 0.14	F=116.45, p=0.0001
Mean leaf litter cover (%) ± s.e.	70.20 ± 3.45	52.31 ± 2.69	F =4.11, p=0.0376
Mean litter depth (cm) ± s.e.	2.01 ± 0.08	1.55 ± 0.05	F =8.33, p=0.0037
Mean debris cover (%) ± s.e	2.05 ± 0.48	8.34 ± 2.73	F=4.39, p=0.0315
Mean coverage of rocks & roots (%) ± s.e.	17.70 ± 4.07	4.25 ± 1.93	F=2.06, p=0.1621

The distribution of quadrats for canopy openness (Figure 6.7), direct and indirect site factors, and leaf-litter cover, was far more variable in SAF than in MPF; the converse was true for the distribution of rocks and roots (Figure 6.8). The shape of the distribution for litter depth was roughly normal and similar for both plot types (Figure 6.9).

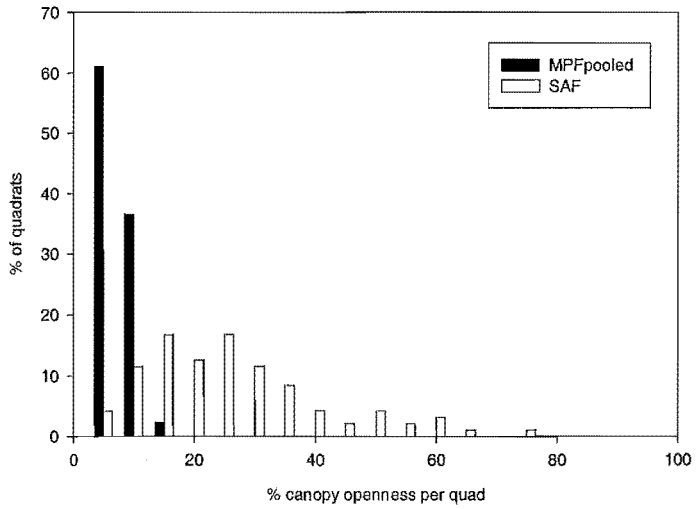


Figure 6.7 The distribution among MPF_{pooled} and SAF quadrats for canopy openness at time 0.

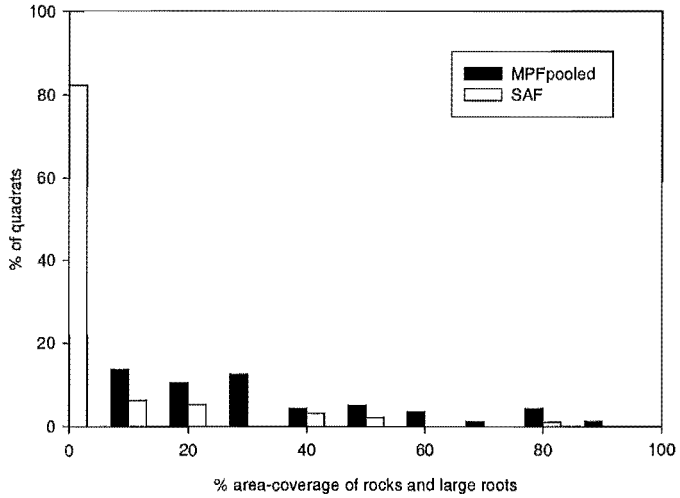


Figure 6.8 The distribution among MPF_{pooled} and SAF quadrats for area coverage of rocks and large roots at time 0.

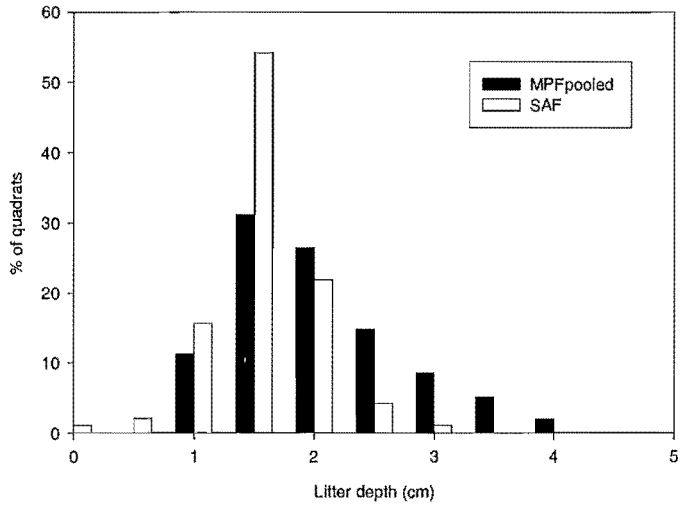


Figure 6.9 The distribution among MPF_{pooled} and SAF quadrats for litter depth at time 0.

Plant characteristics

Species richness: Although there were no significant differences, more species were recorded in SAF than in MPF (Table 6.5). This was largely because SAF contained some remnant forest trees as well as many early-successional, high-light-demanding species that were absent in MPF. In total, 90 species were recorded.

Table 6.5 Species richness in MPF_{pooled} and SAF at time 0.

	Mature-phase forest	Sakau-agro forest
Trees and shrubs	23	28
Lianas	9	10
Herbs and grasses	6	9
Ferns	19	21
Total	57	68
	G (plot type x total no. spp.)=0.965, p>>0.01; G(plot-type x life-form)=0.278, p=0.964	

Presence by life-forms and species:

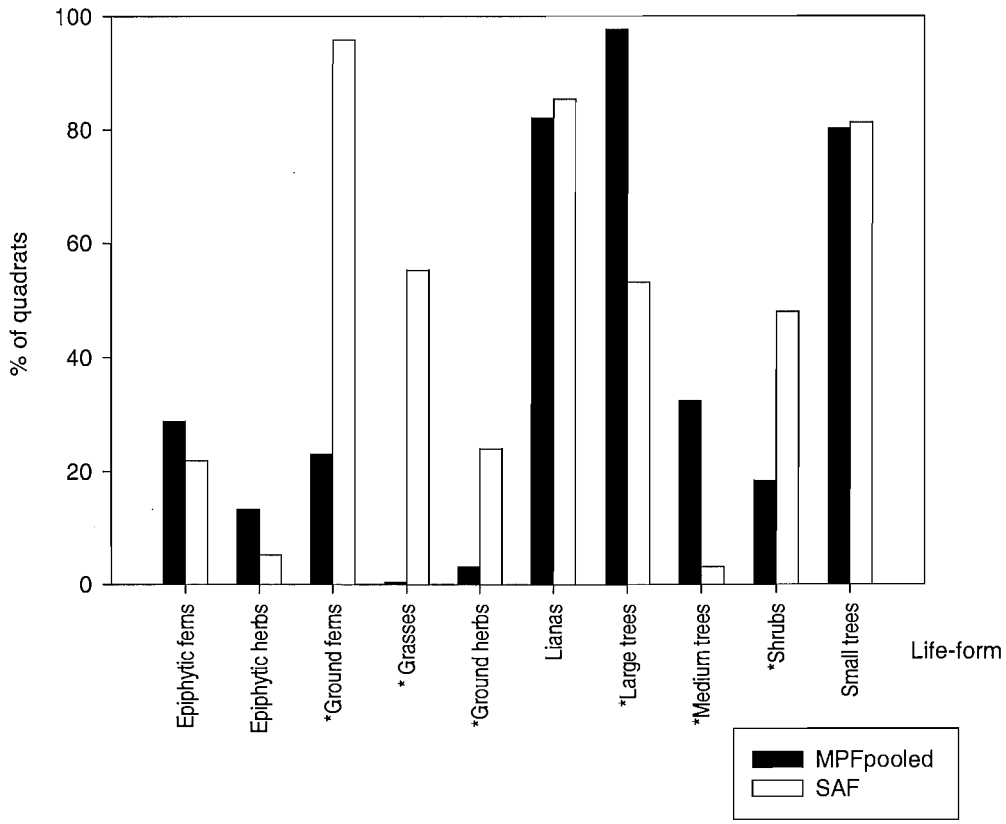


Figure 6.10 Presence of life-forms in MPF_{pooled} & SAF at time 0
Presence is the percentage of quadrats per plot type in which each species occurred. *denotes significant differences in G tests at α=0.01.

Ground ferns, herbs, grasses, and shrubs all occurred in significantly more quadrats in SAF than in MPF (Figure 6.10), while large-tree and medium-tree species occurred in MPF quadrats more than in SAF. For individual species, *Nephrolepis biserrata* (Sw.) Schott, *Cyathea*, *Sphaerostephanos heterocarpus* (Blume) Holttum, *Eragrostis* sp., and *Melastoma malabathricum* var. *marianum* (Naudin) Fosberg occurred in significantly more quadrats in SAF than in MPF ($p<0.01$) (Figure 6.11). *Aglaia*, *Parinari*, *Clinostigma*, *Pachygone ledermanii* Diels, *Myristica*, *Procris pendunculata* (G. Forst.) Wedd., and *Syzygium carolinensis* (Koidz.) Hosok. occurred in significantly more quadrats in MPF than SAF (Figure 6.11). All other recorded species either showed no significant preference towards MPF or SAF, or they occurred in so few quadrats overall that significance tests were not meaningful.

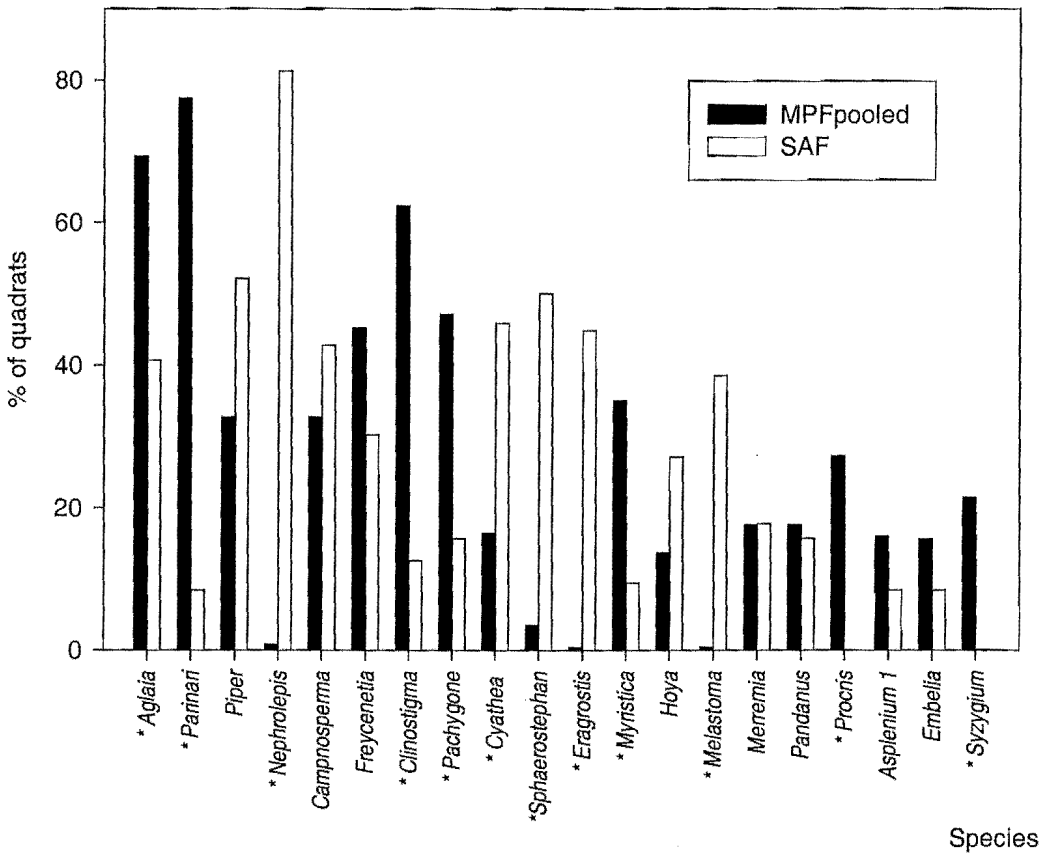


Figure 6.11 Presence of 20 common species in MPF_{pooled} and SAF at time 0.
Species were sorted by combined totals; presence refers to the percentage of quadrats a species occurred in per plot type (full species list in Appendix A), *denotes significant differences in G tests at $\alpha=0.01$.

The underlying trends in species presence with all plot types combined are represented by an ordination (de-trended correlation analysis, DCA) (Figure 6.12a-c).

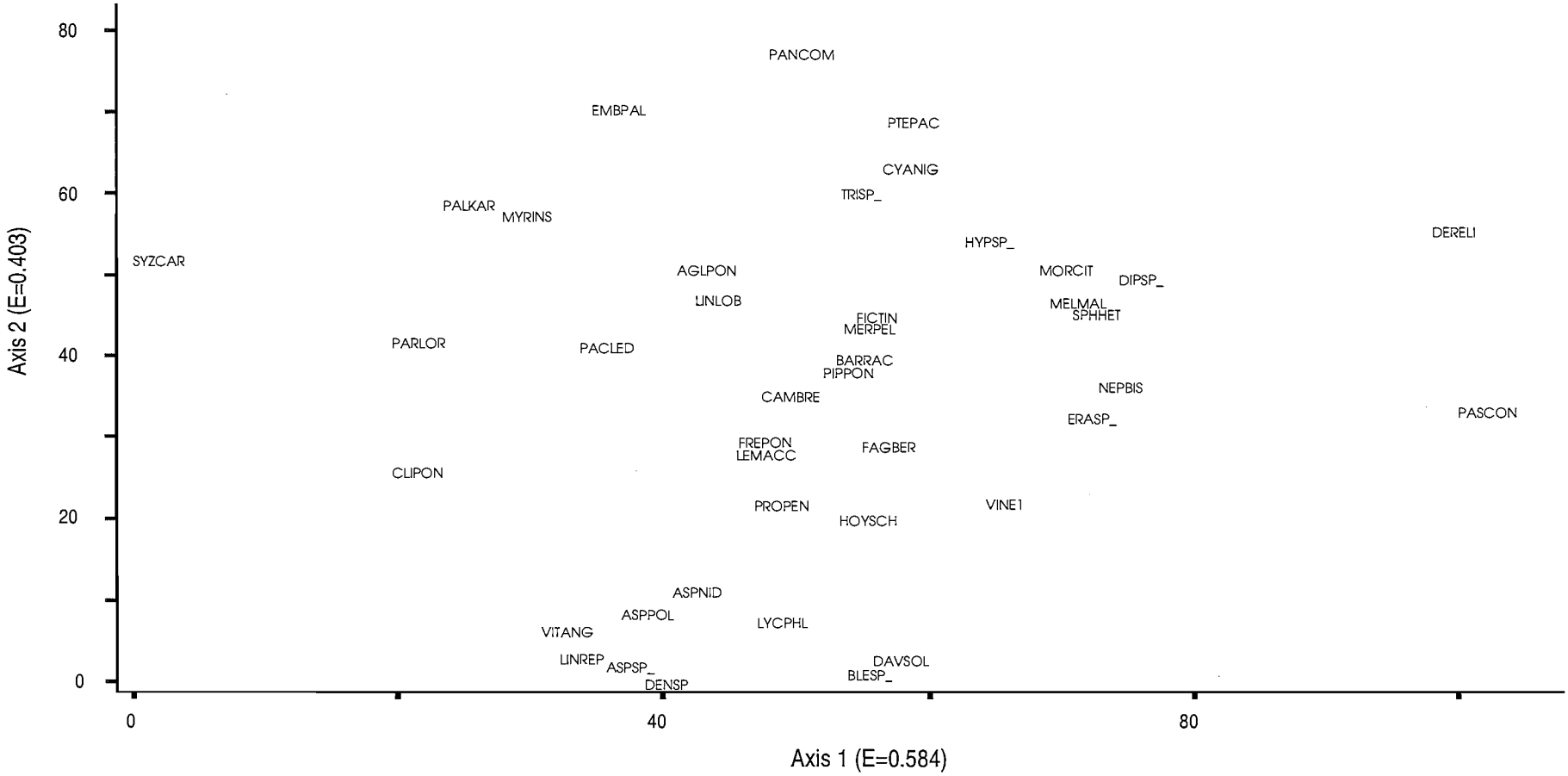


Figure 6.12a De-trended correspondence analysis (DCA): Species presence/absence in quadrats.
Forty-two out of 84 species were excluded because they occurred in fewer than eight quadrats (out of 353). Species abbreviations use the first three letters of the genus then species.

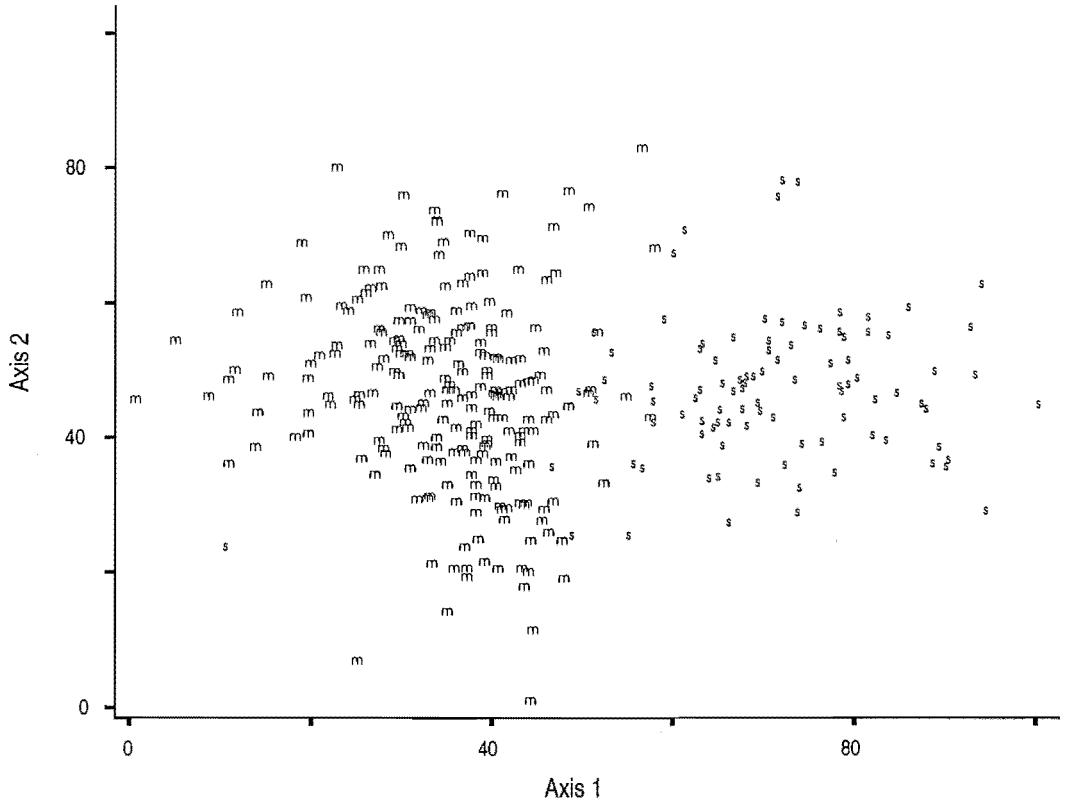


Figure 6.12b DCA: Distribution of quadrats from ordination of species presence/absence.
M=MPF, S=SAF.

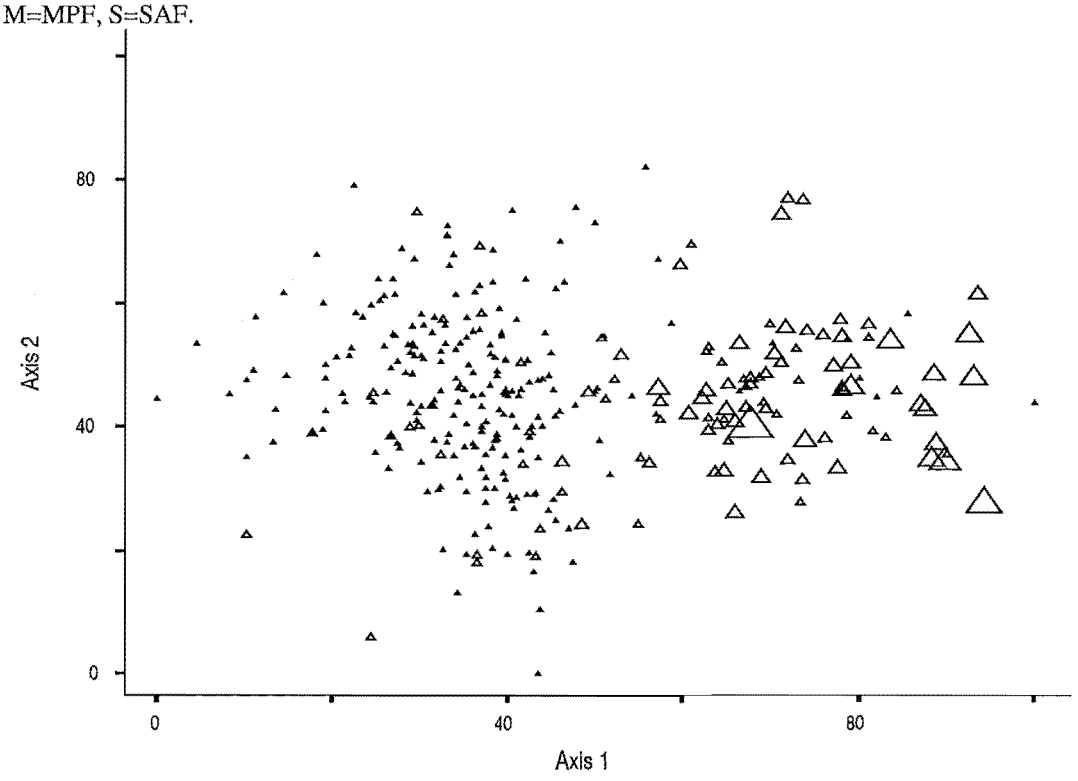


Figure 6.12c DCA: Overlay of canopy openness on quadrat ordination space.
Larger triangles represent higher quadrat canopy openness.

Axis 1 follows a gradient from species and quadrats predominantly occurring in the darker forest quadrats, through to grasses, vines, ferns, and shrubs that are most common in the high-light quadrats in SAF. This axis was correlated with quadrat light measures (Figure 6.12c for canopy openness, Table 6.6) and, to a lesser extent, with litter volume. Axis 2 represents the residual variance not explained in axis 1, but the species arrangement is not related to light or litter (Table 6.6).

Table 6.6 Spearman correlation coefficients for ordination axes of species presence in quadrats.
* denotes that the correlation was significant with $p < 0.01$.

	canopy openness (n=353)	Direct site factor (n=116)	Indirect site factor(n=116)	Litter volume (n=353)
Axis 1	0.5330 *	0.7048 *	0.7093 *	-0.4162 *
Axis 2	0.0075	0.1098	0.0775	-0.1068

Among the epiphytes in Figure 6.12a, epiphytic ferns *Vittaria angustifolia* Blume, *Asplenium polyodon* G.Forst., *Aplenium nidus* L. sensu lato, *Lycopodium phlegmaria* var. *longifolium* Spring, *Lindsaea repens* var. *lingulata* Kramer, and *Asplenium* sp., plus the *Dendrobium* orchids, were tightly grouped in the ordination because they occurred only as epiphytes on large forest trees. In contrast, lianas such as *Hoya schneii* Schltr., *Procris*, *Freycinetia*, and *Piper ponapense* C. D.C. occurred in a wider range of environments.

Trends among non-woody and liana species, including epiphytes, are more clearly seen when analysed without trees and shrubs (Figure 6.13a-b). The species closest to the origin of axis 1 were present almost exclusively in the closed forest. The neighbouring group of species (e.g., *Trichomanes javanicum* var. *boryanum* (Kunze) Fosberg, *Freycinetia*, and *Procris*) occurred predominantly in the forest quadrats but also occurred in more open quadrats. To the right end of axis 1 and in the bottom half of axis 2 occurred species common in SAF. The three lianas, *Merremia peltata* (L.) Merrill, *Piper*, and *Hoya*, occurred commonly in all quadrats, whereas vine1 and *Derris elliptica* (Roxb.) Benth. tended to only occur in the most open quadrats. Both Axes 1 and 2 were correlated with light (Table 6.7).

Table 6.7 Spearman correlation coefficients for non-woody and liana species presence in quadrats.
* denotes a significant correlation at $p < 0.01$, but only coefficients > ~0.45 were considered useful).

	canopy openness (n=353)	Direct site factor (n=116)	Indirect site factor (n=116)	Litter volume (n=353)
Axis 1	0.4752 *	0.6854 *	0.7250 *	-0.3458 *
Axis 2	-0.3699 *	-0.5726 *	-0.5891 *	0.2231 *

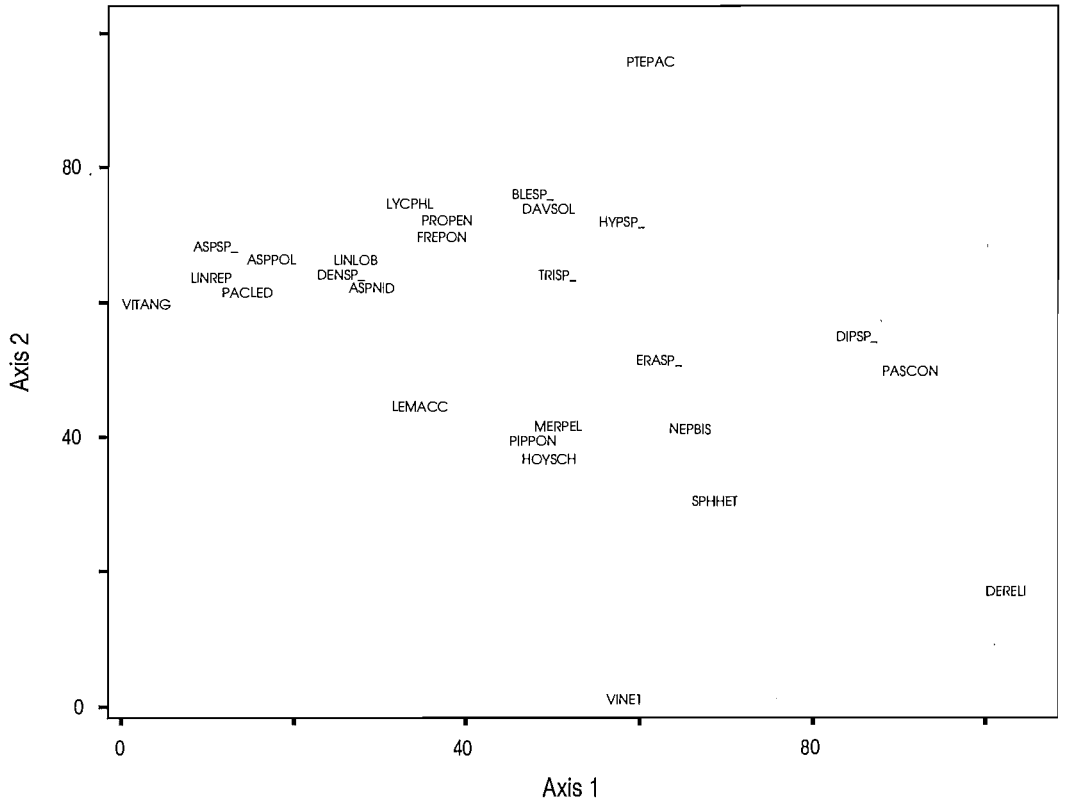


Figure 6.13a DCA: Non-woody and liana species (including epiphytes) presence in quadrats. Species occurring in fewer than eight quadrats were excluded. Species abbreviations use the first three letters of the genus then species.

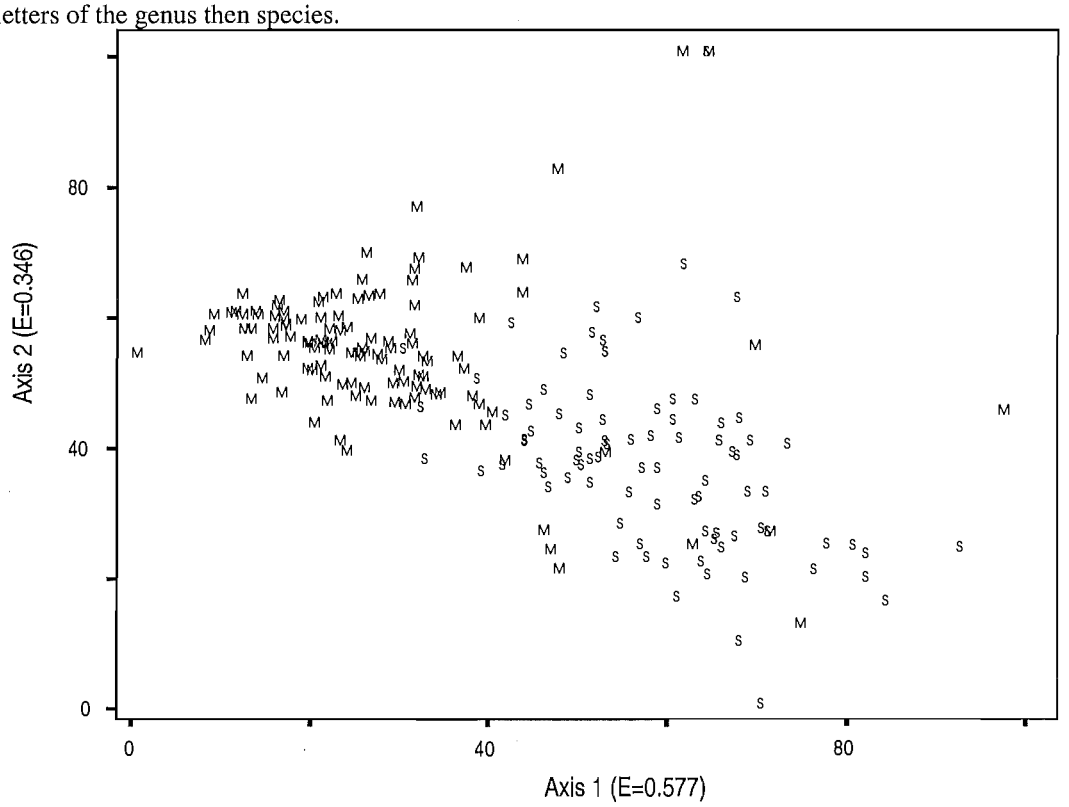


Figure 6.13b DCA: Distribution of quadrats from ordination of non-woody and liana species presence/absence.

Stem frequencies:

SAF contained fewer than half the number of individual trees and shrubs at time 0 compared to MPF (Table 6.8). Seedlings were especially few in SAF compared to MPF, both in absolute numbers (Table 6.8) and as a proportion of the total stems in that plot type (Figure 6.14). There were also fewer large trees but more saplings (individuals with a dbh of at least 1 cm and less than 4 m height) in SAF than in MPF.

Table 6.8 Stem frequencies for tree and shrub species in MPFpooled and SAF at time 0.
Letters denote significant differences between plot types from G tests on data pairs at α=0.01; stem frequencies/m^2 are in brackets.

	Mature-phase forest	Sakau-agro forest	Statistical tests
All individuals combined:	1429 [13.38 ± 0.68]	679 [5.49 ± 1.34]	G=272.71, p<0.001
By Life-form:			
Large tree spp.	1034 a [9.78 ± 0.90]	204 b [1.53 ± 0.47]	G (plot-type x life-form)=464.92, p=0.001
Medium tree spp.	54 a [0.50 ± 0.12]	3 b [0.03 ± 0.02]	
Small tree spp.	309 a [2.80 ± 0.49]	332 a [2.79 ± 0.50]	
Shrub spp.	32 a [0.30 ± 0.11]	140 b [1.15 ± 0.61]	
By Seed-mass group:			
1 (x ≥ 1.0 g)	727 a [6.86 ± 0.84]	67 b [0.58 ± 0.28]	G (plot-type x seed-mass group)=887.32, p=0.001
2 (0.1 g ≤ x < 1.0 g)	590 a [5.49 ± 0.70]	150 b [1.34 ± 0.37]	
3 (0.001 g ≤ x < 0.1 g)	77 a [0.74 ± 0.10]	186 b [1.41 ± 0.53]	
4 (x < 0.001 g)	32 a [0.27 ± 0.07]	261 b [2.02 ± 0.88]	
Unknown seed mass	3	15	
By Size-class:			
Small seedlings	576 a [5.76 ± 0.66]	236 b [2.35 ± 0.88]	G (plot-type x size-class[1])=98.87, p=0.001 [1] large saplings, medium and large trees were combined for testing and freq/m^2.
Seedlings	604 a [6.03 ± 0.63]	218 b [2.19 ± 0.53]	
Large seedlings	93 a [0.93 ± 0.20]	50 b [0.49 ± 0.17]	
Saplings	98 a [0.24 ± 0.03]	149 b [0.37 ± 0.08]	
Large saplings	43 a [0.14 ± 0.02]	25 b [0.06 ± 0.02]	
Medium trees	10	0	
Large trees	4	1	

Interactions of plot type with life-form and seed-mass were highly significant. Approximately 72 % of all trees and shrubs in MPF were large-tree species, compared with only 30 % in SAF. Likewise, over 90 % of all trees and shrubs in MPF had seed-masses in the heaviest two groups (i.e., ≥ 0.1 g) but only 32 % of plants in SAF were species with similar seed-masses.

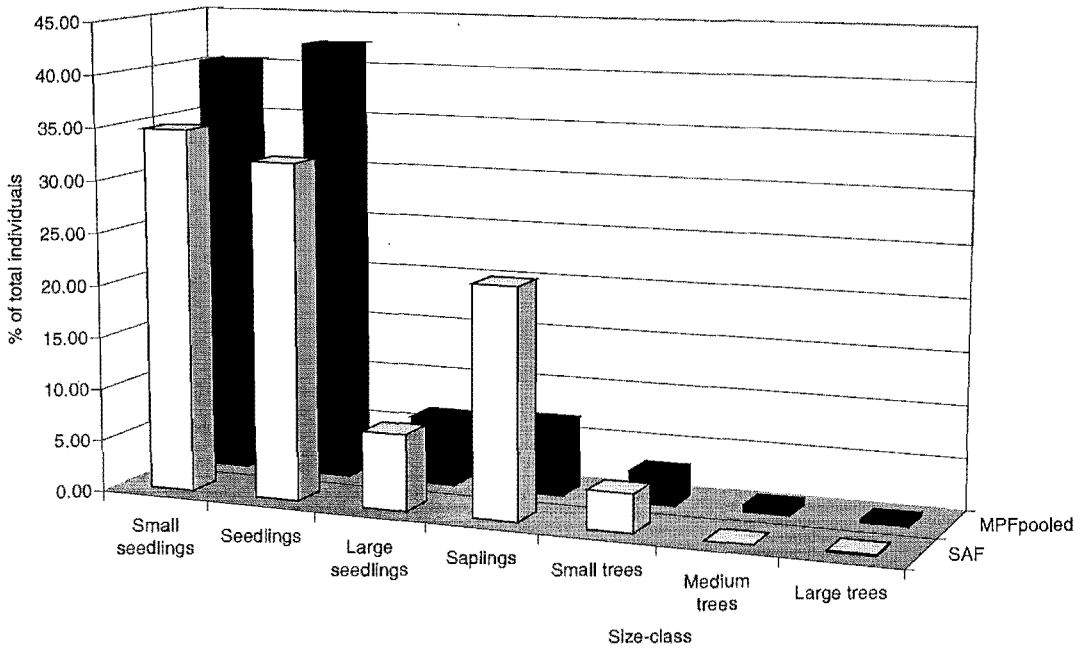


Figure 6.14 Relative size class distribution for stem frequencies in MPF_{pooled} and SAF at time 0. (shows the percentage contribution of each size-class to the total number of individuals)

For individual tree and shrub species, *Campnosperma*, *Cyathea*, *Melastoma*, and *Morinda citrifolia* L. var. *citrifolia* occurred in significantly greater frequencies in SAF than in MPF at time 0, while *Parinari*, *Aglaia*, *Clinostigma*, *Myristica*, *Syzygium*, and *Palaqium* were in greater frequencies in MPF at time 0 (Figure 6.15).

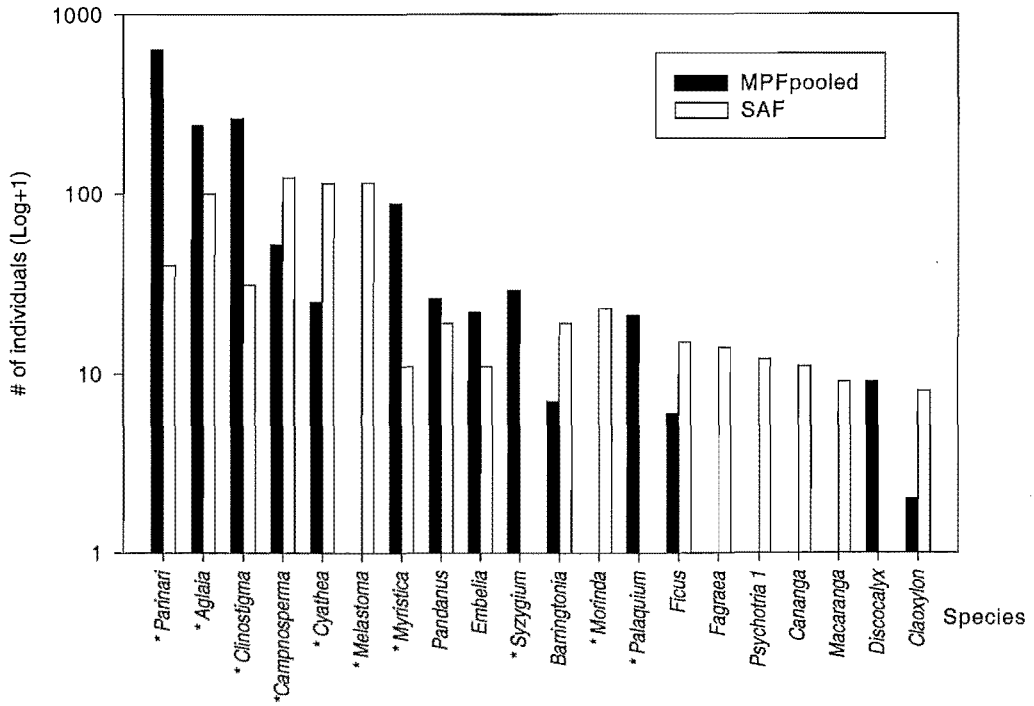


Figure 6.15 Stem frequencies of the twenty most common species in MPF_{pooled} and SAF, time 0.
* denotes a significant single-species G test difference between plot types.

Although six of the ten most common woody species were the same in the two plot types, the species abundance rankings were different (Table 6.9). In MPF, five species accounted for almost 90 % of all individuals recorded in the forest. In contrast, these same species comprised 43 % of the total stocking in SAF. The five most common species in SAF represented about 70 % of total stocking.

Table 6.9 Relative abundance ranks of the ten most common species in MPF_{pooled} & SAF, time 0.
Note: Appendix D shows relative abundance separately for seedlings and saplings.

PLOTTYPE	Mature-phase forest (pooled)			Sakau-agro-forest		
Spp. rank	Species	Frequency	% of total	Species	Frequency	% of total
1	*Parinari*	634	44.40	*Campnosperma*	122	17.97
2	*Clinostigma*	261	18.28	*Melastoma*	114	16.79
3	*Aglaia*	240	16.81	*Cyathea*	113	16.64
4	*Myristica*	87	6.09	*Aglaia*	99	14.58
5	*Campnosperma*	51	3.57	*Parinari*	39	5.74
6	*Syzygium*	28	1.96	*Clinostigma*	30	4.42
7	*Pandanus*	25	1.75	*Morinda*	22	3.24
8	*Cyathea*	24	1.68	*Pandanus*	18	2.65
9	*Embelia*	21	1.47	*Barringtonia*	18	2.65
10	*Palaquium*	20	1.40	*Ficus*	14	2.06
11+	14 SPP.	37	2.59	18 SPP.	90	13.25
	TOTAL	1428	100.00	TOTAL	679	100.00

Quadrat stem frequencies were correlated with direct and indirect site factors (from hemispherical photographs) for all species combined, but the correlations appeared to be driven by a strong negative association between the site factors and stem frequencies of *Parinari* (dominates seed-group 1) (Table 6.10).

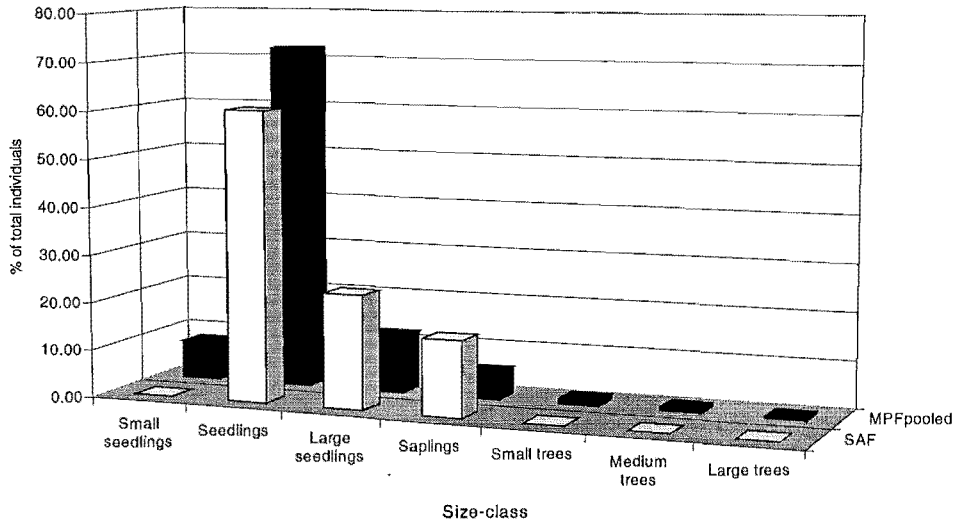
Table 6.10 Spearman's correlation coefficients for seedling stem frequencies in quadrats vs. micro-environmental and non-woody-cover variables.
* denotes a significant correlation at p <0.01, but only coefficients > ~0.45 were considered useful.
All correlations had n=353 quadrats apart from DSFC and ISFC which had n=116.

	Canopy openness	Direct site factor (DSFC)	Indirect site factor (ISFC)	Litter volume	Non-woody species cover
All species	-0.2994 *	-0.5623 *	-0.5412 *	0.2029 *	-0.4180 *
Seed-Gp 1 (x ≥ 1.0 g)	-0.3790 *	-0.5576 *	-0.5984 *	0.3460 *	-0.5464 *
Seed-Gp 2 (0.1 g ≤ x < 1.0 g)	-0.2743 *	-0.4475 *	-0.4288 *	0.1252	-0.3128 *
Seed-Gp 3 (0.001 g ≤ x < 0.1 g)	0.0363	-0.0194	-0.0391	-0.1215	0.0435
Seed-Gp 4 (x < 0.001 g)	0.2352 *	0.3375 *	0.3524 *	-0.2544 *	0.3939 *
Parinari	-0.3779 *	-0.6038 *	-0.6407 *	0.3618 *	-0.5309 *
Aglaia	-0.1569 *	-0.2524 *	-0.3125 *	0.0273	-0.1720 *
Clinostigma	-0.2345 *	-0.4349 *	-0.3537 *	0.1395 *	-0.2814 *
Campnosperma	0.0067	-0.1309	-0.0840	-0.0452	-0.0078

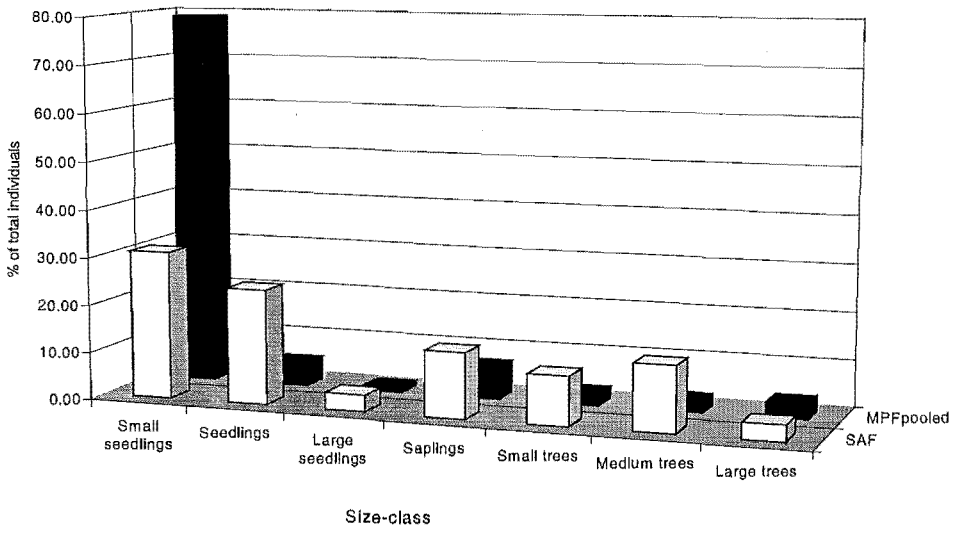
Parinari, *Clinostigma*, and *Campnosperma* were dominant in the canopy of MPF. In comparison to SAF, these species were present not only in much greater numbers in MPF at time 0, but their size-class proportions were also quite different (Figures 6.16a, b, c, respectively). The *Parinari* population in MPF was highly skewed to the large seedling bank, with a decreasing number of larger individuals towards the few large canopy trees. *Parinari* in SAF were mostly seedlings also, but there were greater proportions of large seedlings and saplings, and no large individuals.

In MPF, there appeared to be three main levels of stature for *Clinostigma*: many small seedlings, some saplings, and a few tall trees (Figure 6.16b). In contrast, *Clinostigma* individuals in SAF were scattered across the size-class range, largely a result of remnant individuals remaining after the mature forest was felled and cultivated, and a few small seedlings regenerating under the remnants.

Campnosperma was present in MPF in only two size-classes: a few large canopy trees, and many small seedlings (Figure 6.16c). However, in SAF there were no canopy-sized trees but over a third of the individuals were saplings and 20 % were seedlings 25-100 cm height (compared to none in MPF).



a)



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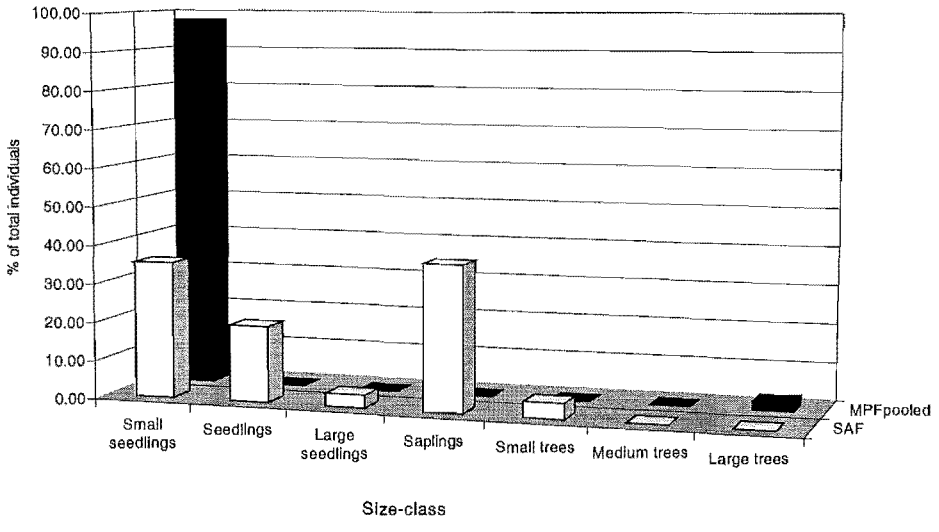


c)

Figure 6.16 Relative size-class distributions for *Parinari*, *Clinostigma* and *Campnosperma* at time 0. % contribution of each size class to the total number of individuals for, a) *Parinari* (total # 634 MPF, 38 SAF); b) *Clinostigma* (total # 261 MPF, 29 SAF); c) *Campnosperma* (total # 51 MPF, 122 SAF).

Health:

A greater proportion of individuals - for both saplings and large seedlings 1-4 m height, and seedlings ≤ 1.0 m height - were classed as healthy in SAF than in MPF (Table 6.11).

Table 6.11 Health of a) seedlings ≤ 1.0 m height, and b) large seedlings and saplings 1-4 m height. Percentages are out of stem frequency totals (less a few individuals with missing data). For valid G tests, frequencies less than 5 became 5, except drought codes which were excluded from G tests because frequencies were so low.

	MPFpooled	SAF	G-test statistic:
a) Seedlings ≤ 1.0 m height:			G (plot-type x healthy
% health [#]	72.11 % [850/1179]	80.32 % [366/455]	vs. not healthy)=13.86,
% physical damage & bent [#]	17.46 % [206]	10.76 % [49]	p=0.001;
% physical damage - not bent [#]	3.89 % [46]	6.86 % [31]	G (plot-type x 3 non-
% biotic coverage [#]	6.40 % [75]	0.69 % [3]	health codes) = 31.97,
% drought-stressed [#]	0.13 % [2]	1.37 % [6]	p=0.001
b) Large seedlings and saplings 1-4 m height:			G (plot-type x healthy
% health [#]	65.45 % [125/191]	84.21 % [167/198]	vs. not healthy)=25.21,
% physical damage & bent [#]	6.91 % [13]	10.53 % [21]	p=0.001;
% physical damage - not bent [#]	2.85 % [5]	1.58 % [3]	G (plot-type x 3 non-
% biotic coverage [#]	24.80 % [47]	1.58 % [3]	health codes) = 33.85,
% drought-stressed [#]	0.0 % [0]	2.11 % [4]	p=0.001

Mean stem height and diameter:

Differences in overall mean stem height or diameter between MPF and SAF at time 0 were not significant (Table 6.12). Mean heights were similar because MPF contained many seedlings but also some very tall trees, whereas SAF was comprised of a higher proportion of saplings than in MPF but few seedlings or tall trees. Heights differed significantly among life-forms, but there were no significant interactions between plot types and life-forms or seed-mass groups. Note, however, that although there were many more large-tree species and species with heavy seeds (seed-group 1) in MPF than in SAF, mean stem height was actually higher for these individuals in SAF than in MPF (Table 6.12).

Table 6.12 Mean stem heights and diameter (at 1.3 m height) in MPF_{pooled} and SAF at time 0. Associated stem frequency totals are in brackets [ ].

MEAN STEM HEIGHT (m):	Mature-phase forest	Sakau-agro forest	Statistical tests
All individuals combined:	1.13 ± 0.05 [1429]	1.31 ± 0.24 [679]	F=0.93, p= 0.4167
By Life-form:			F (plot-type) =1.94, p=0.1530, F(Life-form)=4.87, p=0.0044, F(plot-type x life-form) = 1.29, p=0.2787.
Large tree spp.	1.20 ± 0.06 [1034]	1.86 ± 0.31 [204]	
Medium tree spp.	1.11 ± 0.28 [54]	0.54 ± 0.30[3]	
Small tree spp.	0.83 ± 0.12 [309]	1.09 ± 0.22 [332]	
Shrub spp.	0.38 ± 0.09 [32]	1.23 ± 0.35 [140]	
By Seed-mass group:			F (plot-type) =0.64, p=0.5314, F(seed-mass)=0.18, p=0.9123, F(plot-type x seed-mass) = 0.70, p=0.6474.
1 ($x \geq 1.0$ g)	1.10 ± 0.10 [727]	1.53 ± 0.47 [67]	
2 (0.1 g $\leq x <$ 1.0 g)	1.21 ± 0.15 [590]	1.16 ± 0.23 [150]	
3 (0.001 g $\leq x <$ 0.1 g)	0.96 ± 0.39 [77]	1.23 ± 0.53 [186]	
4 ($x <$ 0.001 g)	1.37 ± 0.30 [32]	1.28 ± 0.39 [261]	
MEAN STEM DIAMETER (cm) (at 1.3 m height), all individuals combined:	8.82 ± 1.10	5.80 ± 2.26	F=2.19, p= 0.1467

In Spearman's correlations of mean height per quadrat for seedlings (all species, by seed-group, and by common species) vs. light and litter measures, only *Campnosperma* produced meaningful correlations. Mean quadrat height of *Campnosperma* was positively associated with canopy openness (coefficient R=0.5296, p=0.0001 (n=107)) and non-woody coverage (R=0.4584, p=0.0001 (n=107)). That is, greater mean heights tended to be associated with more open quadrats and with high quadrat coverage by non-woody species.

Mean percentage cover of non-woody species:

The mean coverage of liana, grass, fern and herb species was very much greater in SAF than in the closed forest, in terms of mean percentage cover and the percentage of quadrats in which non-woody species occurred (Table 6.13). Interaction between plot types and life-forms was highly significant (F(plot-type by life-form)=12.10, p=0.0001): mean percent cover of fern species was over 20 times greater in SAF than in MPF, and grasses, which covered approximately 7 % of the area in SAF, were virtually non-existent in MPF.

Table 6.13 Mean percentage cover of non-woody species, grouped by life-form.

	Mature-phase forest		Sakau-agro-forest		Statistical tests (using type III SS)
	Mean % cover / m^2	% quadrats represented	Mean % cover / m^2	% quadrats represented	
All individuals combined:	2.27 ± 0.51	78	31.54 ± 4.65	100	F=60.61, p=0.0001
By Life-form:					F(plot-type)=79.83, p=0.0001; F(life-form)=24.59, p=0.0001; F(plot-type x life-form) = 9.67, p=0.0001
Ferns	1.14 ± 0.34	26	20.21 ± 3.26	97	
Grasses	0.00	0.4	6.75 ± 3.03	54	
Herbs	0.27 ± 0.16	4	1.50 ± 0.33	25	
Lianas	0.86 ± 0.23	52	3.09 ± 0.80	74	

Total mean cover per quadrat was positively correlated with light, and negatively with litter volume (Table 6.14). That is, high coverage of non-woody species tended to be associated with greater light levels and lower litter volumes.

Table 6.14 Spearman correlation coefficients for non-woody-species cover in quadrats vs. micro-environmental variables.
* denotes a significant correlation at p <0.01. All correlations had n=353 quadrats apart from DSFC and ISFC which had n=116.

	Canopy openness	Direct site factor	Indirect site factor	Litter volume
Mean quadrat non-woody cover	0.4913 *	0.6592 *	0.7042 *	-0.4753 *

The association between light and non-woody cover highly dominated a canonical correlation analysis comparing micro-environmental variables (light, litter volume, debris cover, and rock cover) with plant variables (stem frequency, mean height, mean non-woody cover). The first axis formed from the micro-environmental

variables was dominated by light (standardised canonical coefficients: indirect site factor=0.7891, litter volume = -0.2383, debris = 0.1823, and rocks = -0.0955). The first axis from the plant variables was dominated by non-woody cover (standardised coefficients: stem frequency = -0.1791, mean height = 0.0077, mean non-woody cover = 0.8938). This first pair of canonical correlates explained over 94 % of the association between the two variable sets and accounted for 67 % of the total data variation (R^2).

Mean epiphyte coverage:

Table 6.15 Mean percentage cover of epiphytes per affected tree, grouped by life-form.

	Mature-phase forest		Sakau-agro-forest		Statistical tests (using type III SS)
	Mean % cover / tree	% quadrats represented	Mean % cover / tree	% quadrats represented	
All individuals combined:	5.92 ± 0.79	46	2.83 ± 0.21	29	F=4.42, p=0.0309
By Life-form:					F(plot-type)=9.40, p=0.0002; F(life-form)=117.48, p=0.0001; F(plot-type x life-form) = 2.17, p=0.0392
Ferns	0.61 ± 0.16	25	0.39 ± 0.34	7	
Grasses	0.00	0	0.01 ± 0.01	2	
Herbs	0.40 ± 0.09	12	0.01 ± 0.01	2	
Lianas	4.87 ± 0.62	44	2.40 ± 0.29	27	
Trees and shrubs	0.04 ± 0.02	7	0.01 ± 0.01	2	

Although not significant at α=0.01, mean total epiphyte loads on trees tended to be greater in MPF than in SAF (Table 6.15), and when sub-grouped by life-forms, significant plot-type differences were apparent (F=9.40, p=0.0002). Epiphytes occurred in more MPF quadrats than in SAF mainly because there were more large trees in MPF to provide habitats suitable for epiphytes. This was particularly true for epiphytic ferns and herbs (mostly orchids), which occurred in noticeably more quadrats in MPF than in SAF. Although not significant at α=0.01, ANOVA evidence did point to such an interaction between plot types and life-forms (Table 6.15).

6.2.4 Summary

Figure 6.17 (photo): Typical mature-phase forest

a)

b)

Figure 6.18a-b (photo): Typical sakau-agro forest.
Two sakau plants (heart-shaped leaves) are shown in the foreground of Figure 6.17b.

At time 0, prior to gaps being created, mature-phase forest plots (MPF) were not significantly different from the forest plots that were mature-phase initially but became gap-phase after time 0 (GPF).

The most important differences between sakau-agro-forest (SAF) and mature-phase forest (MPF_{pooled}) at time 0 were:

- Canopy openness was much higher in SAF than in MPF_{pooled}. Leaf litter cover was slightly greater and deeper in mature forest.
- Species richness was slightly higher in SAF than in MPF_{pooled} because a few, remnant forest trees remained and there were many early-successional, high-light-demanding species that were absent in the mature forest. With all plots combined, a total of 90 species was recorded. Presence of individual species in quadrats was correlated with a quadrat light gradient.
- Many more woody individuals (trees and shrubs) occurred in the mature forest than SAF (at least double). Significantly more of these individuals were classed as healthy in SAF than in MPF_{pooled}.
- MPF_{pooled} was dominated by large-tree species and species with heavy seeds. Small-tree and shrub species and species with light seeds were the most common woody species in SAF.
- The most common tree species in MPF_{pooled} were *Parinari*, *Clinostigma*, *Aglaia*, *Myristica*, and *Campnosperma*. In sakau plots, the more common tree/shrub species were *Cyathea*, *Campnosperma*, *Melastoma*, and *Aglaia*. Canopy species with large numbers of seedlings in the mature forest, such as *Parinari* and *Clinostigma*, occurred only rarely as seedlings in regenerating sakau-agro-forest.
- Non-woody (ferns, grasses, herbs) and liana species covered a much greater area in SAF than in MPF_{pooled}. Mean quadrat non-woody cover was positively correlated with light and negatively with litter volume.

Chapter Seven: Forest Changes

a

b

Figure 7.1a-b (photo): Gap-phase forest after a tree (*Campnosperma*) was felled.

This chapter compares if and how the micro-environments and plant responses changed over 15 months in three plot types. Recall that overall, no significant differences were found between GPF and MPF at time 0. Therefore, after gaps were created in GPF plots (e.g., Figure 7.1), the plot types represent i) the mature phase of natural forest (MPF), ii) the gap/regenerative phase of natural forest, that is, the newly created tree-falls (GPF), and iii) sakau-agro-forest as it is regenerating (SAF).

There were three main rainfall-periods during the 15-month study: pre-drought, drought, and post-drought. The El Niño drought lasted from about late December 1997 until late April 1998, but was most severe from January to the end of March. January rainfall, for example, was less than 5 % of the mean January rainfall over the past 17 years (Figure 3.1). One-month re-censuses were conducted in January-February, and the three-month re-censuses in March and April, completed just at the end of the drought. People lit fires in the forest during the drought, largely for fun and often as they walked up to their sakau plots, including one that swept through a plot that was to be studied as GPF (Figure 7.2).

Figure 7.2 (photo): Gap-phase forest plot after a fire swept through the area during the drought. (the plot was excluded from analyses)

Rainfall returned to normal in May and remained high for the 12 months to the final 15-month re-census, promoting recovery and growth (Figures 7.3-7.5).

a)

b)

Figure 7.3 (photo): Regeneration in gap-phase forest 15 months after gaps were created. a) regeneration surrounding the rotting stumps of trees felled after time 0 (plastic forks seen in the photograph were used to hold down identification tags around small seedlings), b) *Clinostigma* regeneration and growth in a space created by a felled tree (log runs lower left to right).

Figure 7.4 (photo): Regeneration in sakau-agro forest 15 months after the initial census. *Nephrolepis*, *Cyathea*, and *Diplazium* are the prominent ferns in the foreground, with *Macaranga* and *Campnosperma* saplings in the background.

Figure 7.5 (photo): Regeneration approximately one year after a GPF plot was burnt accidently. *Macaranga* and *Claoxylon* seedlings, and *Eragrostis* grass, are prominent.

7.1 Micro-environment

7.1.1 Light

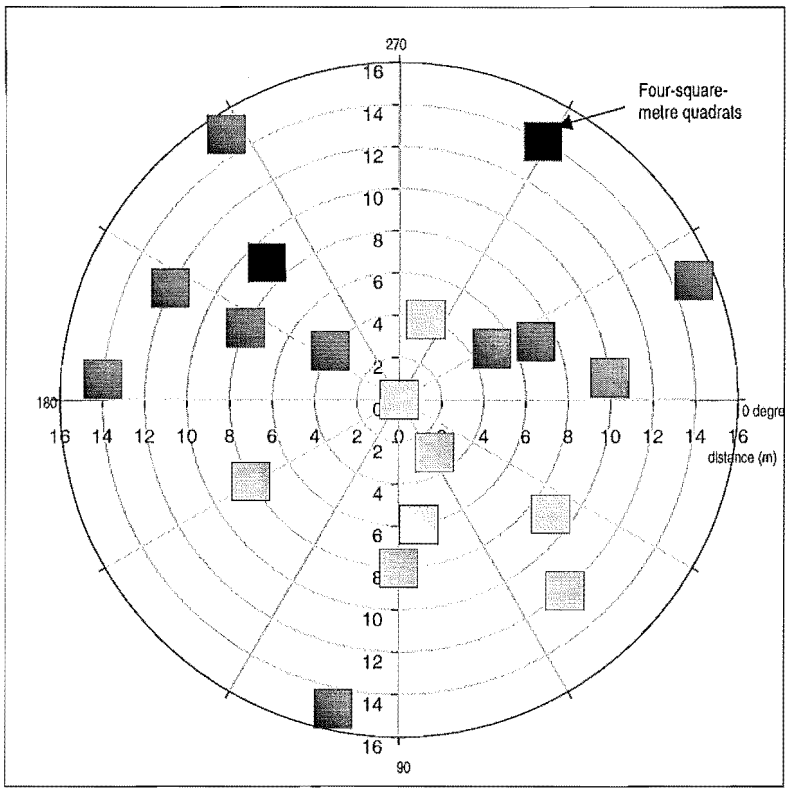
Pre- vs. post-gap light in Gap-phase Forest

Table 7.1 GPF light, pre- and post-gap openings.
Canopy openness was measured with a spherical densiometer, while direct site factor (DSFC) and indirect site factor (ISFC) were calculated from hemispherical photographs.

	Pre-gap	Post-gap
Canopy openness (%) (n=6 plots)	5.26 ± 0.44	7.74 ± 0.71
% direct site factor (%) (n=2 plots)	5.78	5.86
% indirect site factor (%) (n=2 plots)	3.91	3.64

Changes in the GPF light environment after gaps were created were highly variable. Canopy openness calculated from a spherical densiometer tended towards increased light but indirect and direct site factors from hemispherical photographs showed little (or even negative) change.

Mean canopy openness increased following gap formations (Table 7.1). However, with such a small sample size for the analysis, no significant differences were found (pre- vs. post-gap canopy openness, $F=0.72$, $p=0.4438$). Changes varied greatly across the quadrats depending on the location of quadrats in relation to the felled trees (e.g., Figure 7.6). Of 119 GPF quadrats still viable by 15 months, 15 % of quadrats (18) recorded a decrease in canopy openness, 3 % (4) recorded no change, and 82 % (97) recorded an increase in canopy openness. However, in one plot, 12 out of 20 quadrats decreased in canopy openness. Before gaps were created, canopy-openness measures ranged from 2.60 % to 13.0 %. Post-felling, the range expanded to 0 (totally covered by a large tree crown) up to 18.0 %. Relative change per quadrat after gap openings ((canopy openness post-gap - pre-gap)/pre-gap) ranged from -100 % to +110 %.



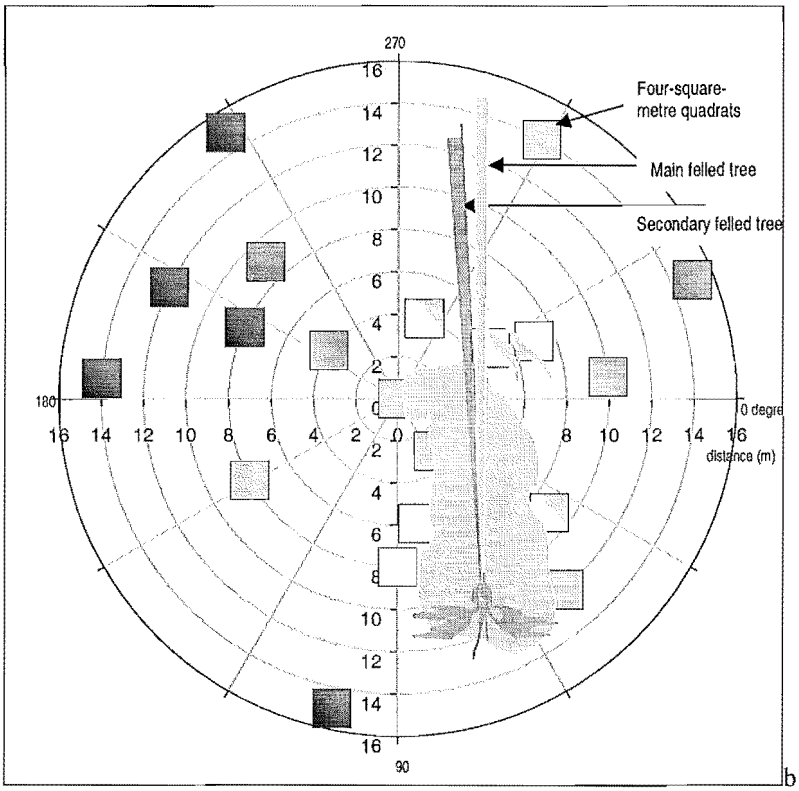
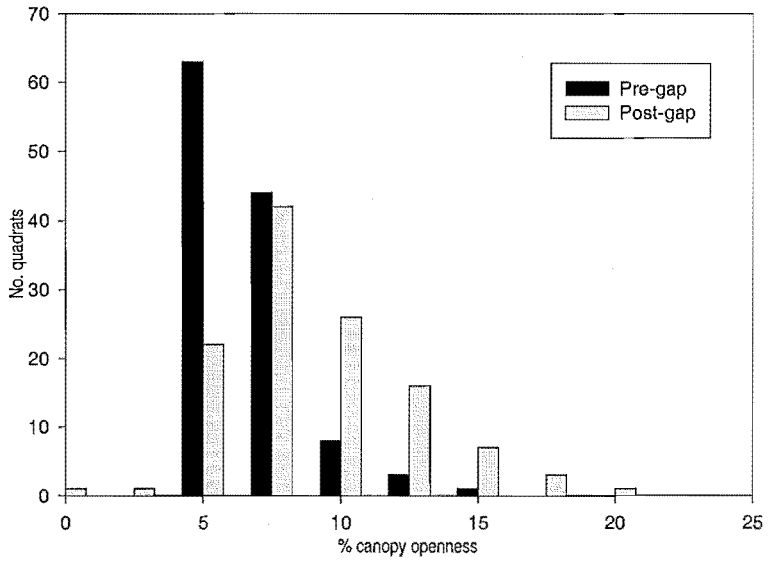


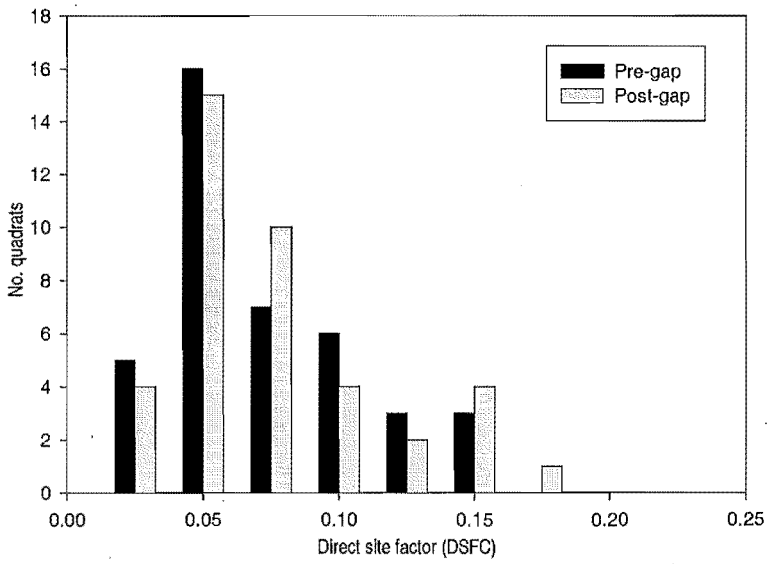
Figure 7.6 Quadrat layout with pre- vs. post-gap light, in GPF plot 15.

a) Shading represents canopy openness **before** trees were felled: darker shaded quadrats have lower canopy openness (down to 3 %) and lighter quadrats have higher canopy openness (up to 13 %).

b) Shading represents canopy openness **after** trees were felled: darker shaded quadrats have lower canopy openness (down to 4 %) and lighter quadrats have higher canopy openness (up to 19 %).



a



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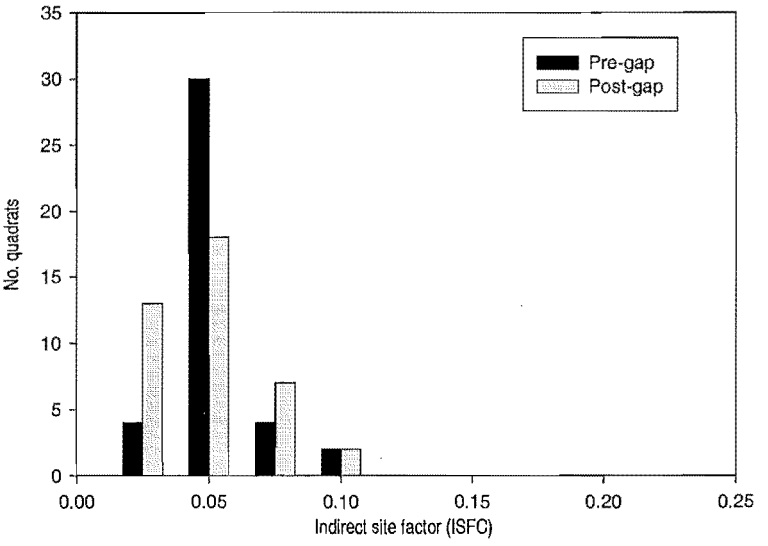

c

Figure 7.7 The light distribution among GPF quadrats pre- and post-gaps
a) canopy openness, b) DSFC, c) ISFC.

For direct site factor with a cosine correction (DSFC) calculated from hemispherical photographs, 46 % of quadrats (18) recorded negative change, 10 % of quadrats (4) no change, and 44 % (17) positive change. In relative change, this equated to a range of -95 % up to +428 %. For ISFC (indirect site factor with cosine correction), 51 % of quadrats (20) recorded negative change, 18 % of quadrats (7) no change, and only 31 % (12) positive change. In relative change this equated to a range of -78 % to +148 %.

The result for canopy openness and DSFC was an increase in the range of light values (Figures 7.7a and b, respectively), but not so for ISFC (Figure 7.7c).

Comparisons among plot types post-gaps

Table 7.2 Light measures among plot types, post-gaps.[14]
Means with the same letter are not significantly different in an LSD test with α=0.01. Note, where there were different LSD results between MPF and GPF with and without SAF in the analysis, the first row gives LSD results for MPF and GPF alone and the second line has all plot types. Photo-papers were measured as the number of papers in a layer that had been bleached by sunlight in a 24-hour period.

	MPF	GPF	SAF	ANOVA statistics
% canopy openness	4.70 % ± 0.31 a	7.74 % ± 0.71 b	24.61 % ± 2.67	MPF vs. GPF: F=17.56,p=0.0015
(n= 18 plots)	a	a	b	All: F=69.27, p=0.0001
% DSFC (n=6 plots)	3.81 % a	5.86 % a	29.72 % b	MPF vs. GPF: F=6.71,p=0.1224
				All: F=120.33, p=0.0014
% ISFC (n=6 plots)	2.67 % a	3.64 % a	21.90 % b	MPF vs. GPF: F=19.57,p=0.0475
				All: F=36.78, p=0.0078
Photo-papers 1 m	3.41 ± 0.10 a	3.82 ± 0.12 b	4.93 ± 0.18	MPF vs. GPF, F=7.13, p=0.0111
(n=59 quadrats)	a	a	b	All: F=31.30, p=0.0001
Photo-papers 3 m	3.41 ± 0.12 a	4.00 ± 0.08 b	5.38 ± 0.14 c	MPF vs. GPF, F=18.50,p=0.0001
(n=58 quadrats)				All: F=73.09, p=0.0001

The light environment differed significantly among the three plot-types after gaps in GPF were created (Table 7.2). LSD tests for all light measures showed sakau plots were very significantly different from MPF and GPF, and GPF was significantly different from MPF for percentage canopy openness and photo-papers.

Photo-paper results found greater differences among the plot types at 3 m than at 1 m (Table 7.2). The number of photo-paper layers bleached by sunlight over 24

[14] Note: MPF and SAF light was measured only at time 0 and I am assuming that it remained relatively constant over 15 months.

hours was significantly greater at 3 m than at 1 m (ANOVA: F=34.41, p=0.0001, n=58). Although there was no significant interaction among plot types (F=2.18, p=0.1238), separate analyses did find that differences between 1 m and 3 m light stacks were greater in SAF and GPF quadrats (p=0.0002, 0.0025, respectively) than in MPF (p=0.0339, non-significant at 0.01 level).

Comparisons among one-metre light measures

Light measures were well correlated with each other over all quadrats (Table 7.3a) and in the highly opened SAF quadrats (Table 7.3c), but they were less congruous in the lower light range of MPF and GPF (Table 7.3b). That is, the less open the canopy, the weaker the correlations. For example, Spearman's correlations

Table 7.3 Spearman's rank correlation coefficients between pairs of quadrat light measurements, post-gaps.
a) **All plot types included** (N=116 for measures involving hemispherical photographs, and 59 for photo-papers). All correlations were significant at p <0.01.
b) **SAF excluded** (n=78 and 40). All correlations were significant at p < 0.01.
c) **SAF only** (n=38 and 18). All correlations were significant at p < 0.01.

a)	Canopy openness	Direct site factor (DSFC)	Indirect site factor (ISFC)	Photo papers at 1 m
Canopy openness	1.0000			
DSFC	0.7759	1.0000		
ISFC	0.7929	0.9211	1.0000	
Photo papers 1 m	0.7469	0.8278	0.7846	1.0000
b)	**canopy openness**	**DSFC**	**ISFC**	**Photo papers at 1 m**
Canopy openness	1.0000			
DSFC	0.5917	1.0000		
ISFC	0.6283	0.8220	1.0000	
Photo papers 1 m	0.4692	0.6614	0.5034	1.0000
c)	**canopy openness**	**DSFC**	**ISFC**	**Photo papers at 1 m**
Canopy openness	1.0000			
DSFC	0.8246	1.0000		
ISFC	0.8401	0.9654	1.0000	
Photo papers 1 m	0.7340	0.7942	0.7416	1.0000

between canopy openness and the hemishperical-photograph measures were less than R= 0.20 for all quadrats with canopy openness less than 5.0 %. The two light measures derived from hemispherical photographs – direct site factor and indirect site factor – were, not surprisingly, highly correlated with each other (Table 7.3). Overall and in low light, the photo papers were better correlated with direct site factor than canopy openness from the spherical densiometer, but canopy openness was better correlated with indirect site factor in both high and low light. Note that although hemispherical photo results were only taken in a sub-sample of plots, canopy openness by the densiometer in the same sub-sample of plots produced similar results to the full densiometer sample.

Spearman's correlations of the different light measures with plant variables later in this chapter and in the previous chapter showed that in general quadrat DSFC and ISFC were the best correlates for quadrat plant responses, especially for stem frequencies, species presence, and mean non-woody cover analyses. Both hemispherical-photograph measures produced similar correlations but ISFC tended to be the slightly stronger correlate. Canopy openness from the spherical densiometer was weak in comparison to the other measures for new recruitment totals per quadrat vs. light, but fared better in some mean height and growth analyses, although this may have been due to small sample sizes for the other (sub-sampled) light measures.

These results suggest that DSFC and ISFC measures derived from hemispherical photographs more realistically reflected the complex living environment for plants in this study as depicted in the quadrat data, than either canopy openness from the spherical densiometer or light-sensitive photo papers. Although all measures performed worse in the low light conditions of gap and mature forest, photo papers and canopy openness appeared to deteriorate the most.

Hemispherical photographs can be analysed to give various measures of canopy gap morphology, direct and indirect site factors being two common ones. They are generally considered to be quick, objective, and provide permanent records of canopy architecture (Rich 1990). They are far from perfect, however. Like the other measures used in this study, hemispherical photographs were considerably less powerful as correlates in the low light conditions presented in mature-phase and most of gap-phase forest (Table 7.3, also see Rich 1990; Whitmore et al. 1993). Also, present analysis systems do not allow for light transmission and reflection from leaves, that is, pixels on

the photograph are either black (completely blocked by one or many leaves) or white (clear sky) (Roxburgh & Kelly 1996). Where vegetation was dense in SAF in the first two metres above the ground but unobstructed above that, one fern or palm frond may have covered all the photo area but then snapped or died, leaving the quadrat area completely open. In contrast, light was filtered through a much taller canopy height in the forest plots.

In spite of Rich's (1990) comments about the speed and ease of hemispherical photography, probably in relation to a large sample size of more accurate but more expensive quantum sensors, canopy openness from a spherical densiometer was far quicker, easier, and cheaper than hemispherical photographs. Results in this chapter and the previous one indicate that canopy openness (and photo papers) was an effective indicator of plot-mean light environments, but considerably less accurate for quadrat light. Spherical densiometers have been used successfully elsewhere (e.g., Raich & Gong 1990).

Canopy openness is therefore a simple, fast, and effective indicator of the light environment over a broad range of light environments, for example, comparisons of gap-centre light levels as used by Raich and Gong (1990), or my plot-mean comparisons between forest and SAF. However, hemispherical photographs or quantum sensors are much better measures than a spherical densiometer where relatively high resolution and detailed light estimates are required, such as my quadrat analyses or physiological studies.

7.1.2 Leaf-litter cover (0-3 months)

Table 7.4 Leaf-litter cover per m^2 (± standard error) over three months.

	Time 0	1 month	3 months	Test statistics: MPF vs. GPF	Test statistics: all plot types
MPF	70.77 % ± 4.43	70.30 % ± 4.52	70.32 % ± 4.63	Plot type:F=0.06,	Plot type:F=3.21,
GPF	69.54 % ± 5.84	67.54 % ± 6.95	67.46 % ± 6.91	p=0.8058;	p=0.0689;
SAF	52.31 % ± 2.69	.	53.22 % ± 3.13	Time: F=2.17, p=0.1646;	Time: F=1.59, p=0.2386;
				Time*plot type: F=1.08,	Time*plot type: F=1.02,
				p=0.3769	p=0.4156

The area covered by leaf litter, initially (non-significantly) lower in SAF than in the forest plots (p=0.0376, Table 6.4), changed very little in the first three months of the study (Table 7.4).

7.1.3 Litter depth (0-15 months)

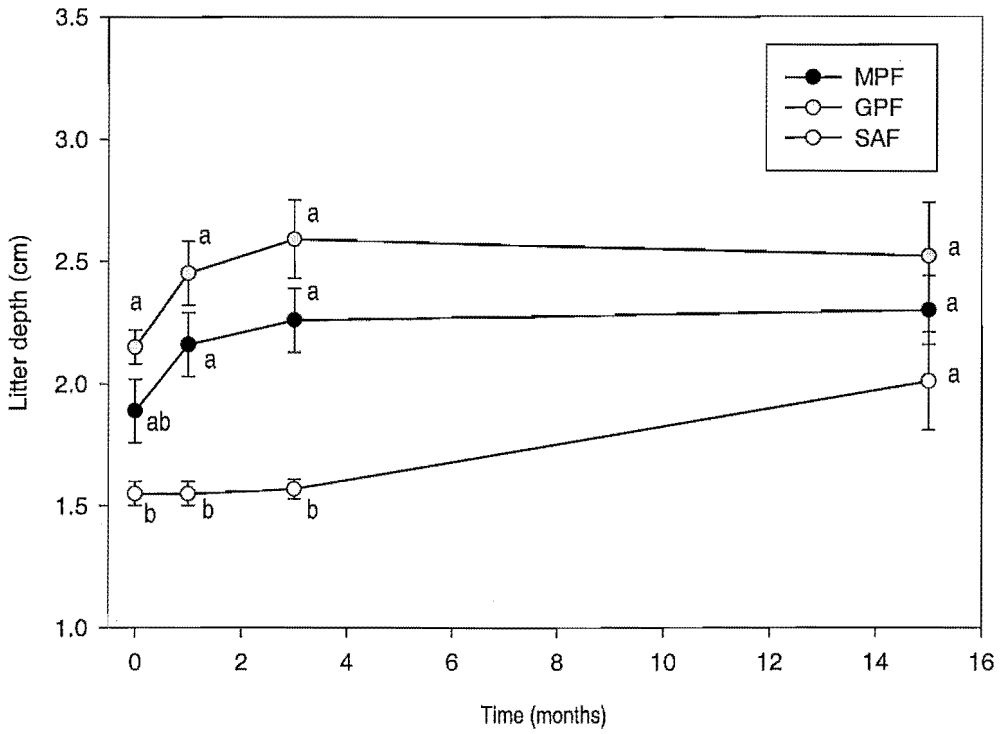

Figure 7.8 Mean litter depth over 15 months.
Means with the same letter were not significantly different in an LSD test with α=0.01.

Overall, litter depths changed over time (time: F=10.01, p=0.0011; Figure 7.8), but the patterns of change by the forest plot types vs. SAF were not significantly

different (time x plot type: F=1.79, p=0.1398), and no significant differences were found between MPF and GPF alone.

The increases in litter depths in both MPF and GPF over 0-3 months were probably related to the drought. Trees lost more leaves and litter-decomposition rates may have been slower during the worst of the drought. In contrast, the noticeable increase in SAF litter depths appeared to be related to successional changes as many open grassy areas were shaded by taller ferns and rapidly colonising trees and shrubs.

With an increase in forest litter depths during the drought months, we might have also expected to see some increase in leaf-litter cover. The lack of change in leaf-litter cover in forest plots (Table 7.4) is likely to be because in forests approximately 85 % (85 %, 86 %, and 55 % for MPF, GPF, and SAF) of the area was already covered with leaf litter, after rocks and large buttress roots were excluded. Hence only a small area of bare ground was potentially available for additional leaf litter coverage.

7.1.4 Debris (0-3 months)

Table 7.5 Woody debris (branches, logs, etc.) cover per m^2 over three months.
Different letters denote significant differences between MPF and GPF in an LSD test with α=0.01 (means were not significantly different when all three plot types were included in an LSD test).

	Time 0	1 month	3 months	Test statistics: MPF vs. GPF	Test statistics: all plot types
MPF	3.13 % ± 0.63	3.20 % ± 0.63	3.27 % ± 0.65	Plot type:F=5.52,	Plot type:F=1.71,
	a	a	a	p=0.0386;	p=0.2136;
GPF	0.80 % ± 0.20	10.61 % ± 1.17	10.61 % ± 1.17	Time: F=56.23, p=0.0001;	Time: F=48.28, p=0.0001;
	a	b	b	Time*plot type: F=56.23,	Time*plot type: F=20.41,
SAF	8.34 % ± 2.73	.	8.54 % ± 2.67	p=0.0001	p=0.0001

Unsurprisingly, the area of each quadrat covered by woody debris increased dramatically in GPF after gaps were created but remained fairly similar in MPF and SAF (Table 7.5). Almost 30 % of the 119 GPF quadrats (35) recorded increased debris cover after the trees were felled, with nine quadrats increasing from minimal debris to 50 % or greater quadrat cover (up to 90 %).

7.2 Plants: Tree and Shrub Species

7.2.1 Stem frequencies over time

The total number of stems in MPF and GPF changed significantly over time (time: MPF Gadj=49.73, $p<0.001$; GPF Gadj=58.37, $p<0.001$). Frequencies decreased through the second and third censuses, strongly affected by the drought, then increased through the post-drought year (3-15 months) to the fourth census (Figure 7.9). Although the stem population was slightly (but not significantly) greater in GPF than in MPF by 15 months, the patterns of change over the 15 months were similar (CATMOD, plot type x time: $X^2=2.01$, $p=0.5705$, no significant time contrasts for 3-15 months). In contrast to the forest plot types, the number of stems in SAF at each census did not fluctuate during the drought or in the year after (time: Gadj=0.30, $p>0.75$).

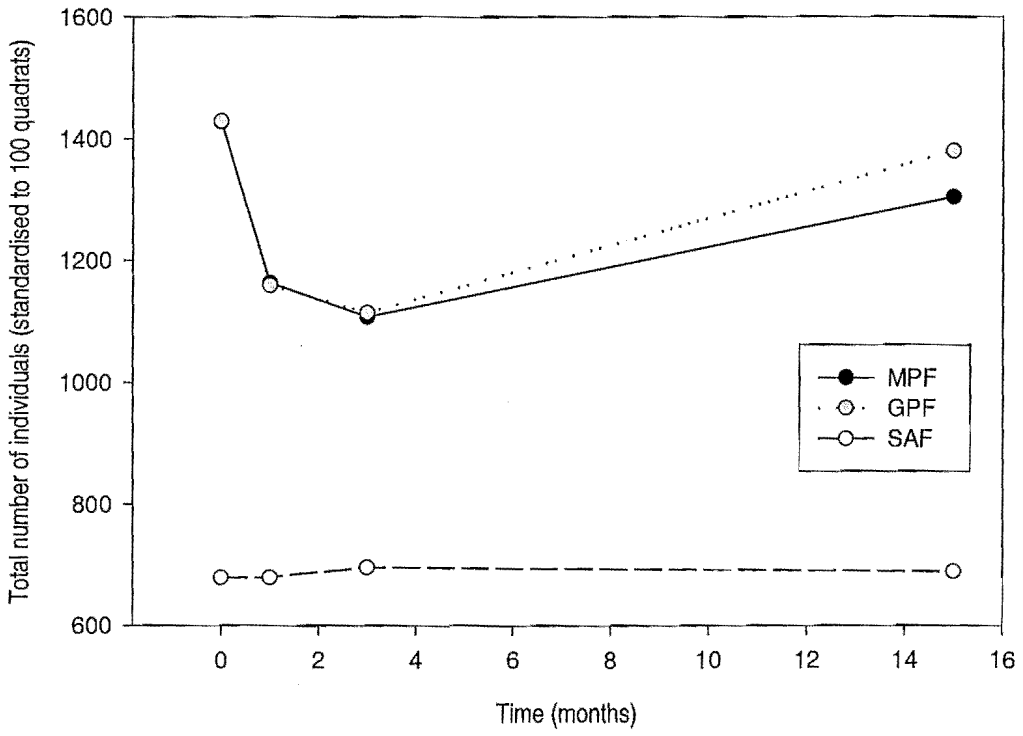

Figure 7.9 Total stem frequencies among plot types over 15 months.
Note: The MPF graph line for 0-3 months lies under that for GPF.

Table 7.6 Changes in stem frequencies over 15 months, all individuals combined, by size-class.
Note that trees taller than 10 m are not shown by size-class, but their frequencies changed very little over 15 months. % mortality is the number dead out of the previous census total (e.g., deadt0-1/ present t0). Recruitment ratio (no. new recruits/ total stock at previous census) is in brackets [ ] after new recruits stem frequency. # denotes a significant difference (adjusted G with $p<0.01$) in stem frequency between MPF and GPF, * MPF vs. SAF, and + GPF vs. SAF.

	Present	Dead	New 0-1	Present	Dead	New	Growth	Present	Dead	New	Growth	Present	Statistical tests
All individuals combined:	T0	0-1 month [%]	month	1 month	1-3 mo. [%]	1-3 mo.	1-3 mo.	3 mo.	3-15 mo. [%]	3-15 mo.	3-15 mo.	15 mo.	
MPF	1428	300 [21.0 %]	35 [2.4 %]	1163	99 [8.5 %]	42 [3.6 %]	.	1107	154 [13.9 %]	351 [31.7 %]	.	1304	Plot type x time:
GPF	1429+	338 [23.6 %]	68 [4.8 %]	1159+	121 [10.4 %]	76 [6.6 %]	.	1114+	236 [21.2 %]	502 [45.0 %]	.	1380+	MPF/GPF:X^2=2.01, p=0.5705;
SAF	679*	.	.	679*	80 [11.8 %]	97 [14.3 %]	.	696*	193 [27.7 %]	185 [26.6 %]	.	689*	All: X^2=27.40, p=0.0001
By size-class:													
Small seedlings (Individuals ≤ 25 cm height)													
MPF	510#	216 [42.3 %]	22 [4.4 %]	317#	62 [19.7 %]	36 [11.4 %]	-4	288#	72 [24.9 %]	236 [82.1 %]	+17	468#	*Time:*
GPF	650+	287 [44.1 %]	54 [8.3 %]	417+	84 [20.2 %]	66 [15.9 %]	-1	398+	152 [38.2 %]	415 [104 %]	+8	669+	MPF/GPF:X^2=12.32,
SAF	234*	.	.	234*	54 [23.1 %]	86 [36.9 %]	-11	255	133 [52.2 %]	117 [45.7 %]	-16	223*	p=0.0064;
Seedlings (Individuals ≤ 100 cm height but > 25 cm)													All: X^2=13.10, p=0.0044.
MPF	636	80 [12.5 %]	12 [1.9 %]	569	33 [5.9 %]	3 [0.5 %]	-4	535	75 [14.1 %]	113 [21.1 %]	-17	556	*Plot type x time:*
GPF	568+	48 [8.4 %]	13 [2.4 %]	534+	34 [6.5 %]	10 [1.9 %]	+7	516+	78 [15.1 %]	86 [16.6 %]	-15	508+	MPF/GPF:X^2=0.38, =0.9439;
SAF	218*	.	.	218*	18 [8.1 %]	7 [3.3 %]	-2	205*	36 [17.8 %]	7 [3.6 %]	-16	160*	All: X^2=5.98, p=0.4258.
Large seedlings (Individuals 1-4 m height but < 1 cm diameter)													*Size-class x time:*
MPF	111#	1 [0.7 %]	0	110#	1 [1.3 %]	0	+5	114#	4 [3.2 %]	0	+1	112#	MPF/GPF:X^2=146.44,
GPF	75	1 [1.1 %]	0	74	0	0	-2	72	5 [7.0 %]	0	+4	71	p=0.0001;
SAF	50*	.	.	50*	1 [2.1 %]	0	+15	64*	3 [4.9 %]	0	+2	63*	All: X^2=80.98, p=0.0001.
Saplings (Individuals with heights 1-4 m but diameter ≥ 1 cm; or for monocot trees, height ≥ 1.5 m, no diameter specified)													*Plot type x size-class x time:*
MPF	108	3 [2.7 %]	0	105	1 [0.7 %]	3 [2.8 %]	+1	108	2 [2.0 %]	1 [1.3 %]	-4	103	MPF/GPF:X^2=3.96, p=0.9841;
GPF	87+	0	1 [1.0 %]	87+	3 [2.9 %]	0	-8	76+	1 [1.1 %]	1 [1.1 %]	0	76+	All: X^2=61.33, p=0.0001.
SAF	150*	.	.	150*	7 [4.9 %]	3 [2.1 %]	-2	144	20 [13.8 %]	61 [42.8 %]	+7	193*	
Large saplings (Individuals with heights 4-10 m)													
MPF	36	1 [2.0 %]	0	36	1 [2.0 %]	0	+2	37	0	0	+1	38	
GPF	18	0	0	18	0	0	+4	22	0	0	+3	24	
SAF	21	.	.	21	0	0	+1	22	0	0	+21	43	

Most of the changes in frequencies occurred within the seedling classes (Table 7.6), particularly small seedlings ≤ 25 cm in height. Sapling increases in SAF related to growth of individuals into the four-metre-square quadrat for the ≥ 1 cm dbh measurement class, particularly *Melastoma*. G-tests for each census and size class highlight how variable the plot types were at the start within each species sub-group, even between MPF and GPF. Yet, when each size class was analysed, no significant G test plot-type-by-time interactions were found between MPF and GPF, and among the three forests, only small seedlings ≤ 25 cm tall showed a significant interaction among plot types and time (G=61.81, p=0.001). That is, relative differences among plot types with respect to numbers of trees and shrubs in each size class remained fairly similar over the 15 months, even though the absolute frequencies for each plot type changed. Small seedlings, especially *Campnosperma* and *Clinostigma*, were more susceptible to drought so they decreased relative to the larger seedlings such as *Parinari* that were better able to withstand dry conditions.

Comparing MPF and GPF with respect to life-form categories, large-tree species in both plot types followed the drought pattern of loss over 0-3 months and recuperation post-drought to 15 months (Table 7.7). Medium- and small-tree species showed similar patterns but mortality was not quite so pronounced in the first month, compared to large-tree species. The significantly different response among life-forms over time was largely attributable to the large-tree species *Clinostigma* and *Campnosperma*, whose seedling populations were severely affected by the drought (Table 7.9a). However, there were no significantly different responses over time between MPF and GPF, nor were there among all three plot types, despite life-forms in SAF not showing the same high mortality and lack of regeneration during the drought as the forest plots (Table 7.7). Only large-tree species showed any relative change in numbers among the plot types (plot type x time: MPF vs. GPF G=3.64, p=0.303; all plot types G=23.23, p=0.001).

Significant interactions between MPF and GPF with respect to seed mass groups over time (Table 7.8) mostly related to seed-group-3 species (those with small-medium seed mass) (seed group 3, plot type x time G=22.23, p=0.001; groups 1, 2, and 4 were all highly insignificant). By the 15-month re-census, seed-group 3 species were

Table 7.7 Changes in stem frequencies over 15 months by life-form.
% mortality is the number dead out of the previous census total (e.g., deadt0-1/ present t0). Recruitment ratio (no. new recruits/ total at previous census) is in brackets [ ] after new recruits stem frequency. # denotes a significant difference (adjusted G with p<0.01) in stem frequency between MPF and GPF, * MPF vs. SAF, and + GPF vs. SAF.

	Present T0	Dead 0-1 month	New 0-1 month	Present 1 month	Dead 1-3 mo.	New 1-3 mo.	Present 3 mo.	Dead 3-15 mo.	New 3-15 mo.	Present 15 mo.	Statistical tests
By life-form:											
Large tree spp.											
MPF	1029	262 [25.4 %]	23 [2.3 %]	791	70 [8.9 %]	29 [3.7 %]	750	126 [16.8 %]	259 [34.6 %]	883	*Time:*
GPF	1040+	306 [29.4 %]	65 [5.3 %]	789+	102 [12.9 %]	68 [8.6 %]	755+	182 [24.0 %]	398 [52.7 %]	972+	MPF/GPF:X^2=9.27, p=0.0259;
SAF	204*	.	.	204*	40 [19.4 %]	68 [33.2 %]	232*	96 [41.3 %]	88 [37.7 %]	224*	All: X^2=1.41, p=0.7022.
Medium tree spp.											*Plot type x time:*
MPF	65	6 [8.9 %]	4 [5.6 %]	63	9 [13.8 %]	2 [3.4 %]	57	6 [10.3 %]	26 [46.2 %]	77#	MPF/GPF:X^2=0.01, p=0.9997;
GPF	41+	2 [4.1 %]	1 [2.0 %]	40+	1 [2.1 %]	1 [2.1 %]	40+	4 [10.4 %]	9 [22.9 %]	45+	All: X^2=1.09, p=0.9818.
SAF	3*	.	.	3*	1 [33.3 %]	0	2*	0	0	2*	*Life-form x time:*
Small tree spp.											MPF/GPF:X^2=24.61, p=0.0034;
MPF	297	32 [10.7 %]	5 [1.7 %]	270	18 [6.7 %]	4 [1.3 %]	256	14 [5.4 %]	61 [23.8 %]	303	All: X^2=10.64, p=0.3012.
GPF	322	29 [9.1 %]	12 [3.1 %]	303	18 [5.8 %]	7 [2.2 %]	292	45 [15.6 %]	88 [30.3 %]	334	*Plot type x life-form x time:*
SAF	332	.	.	332	26 [7.8 %]	25 [7.5 %]	331*	46 [13.8 %]	70 [21.1 %]	355	MPF/GPF:X^2=2.61, p=0.9777;
Shrub spp.											All: X^2=16.34, p=0.5690.
MPF	37	1 [2.0 %]	3 [7.8 %]	39	1 [3.7 %]	7 [18.5 %]	45	8 [17.7 %]	4 [9.7 %]	41	
GPF	25+	1 [3.3 %]	3 [10.0 %]	27+	1 [3.1 %]	1 [3.1 %]	27+	5 [18.8 %]	6 [21.9 %]	28+	
SAF	140*	.	.	140*	14 [9.7 %]	4 [3.0 %]	130*	51 [39.2 %]	28 [21.6 %]	107*	

Table 7.8 Changes in stem frequencies over 15 months, by seed-mass groups.
% mortality is the number dead out of the previous census total (e.g., deadt0-1/ present t0). Recruitment ratio (no. new recruits/ total at previous census) is in brackets [ ] after new recruits stem frequency. # denotes a significant difference (adjusted G with p<0.01) in stem frequency between MPF and GPF, * MPF vs. SAF, and + GPF vs. SAF.

	Present T0	Dead 0-1 month	New 0-1 month	Present 1 month	Dead 1-3 mo.	New 1-3 mo.	Present 3 mo.	Dead 3-15 mo.	New 3-15 mo.	Present 15 mo.	Statistical tests
By Seed-mass group:											
1 (x ≥ 1.0 g)											
MPF	788#	100 [12.7 %]	15 [1.9 %]	703#	38 [5.5 %]	7 [1.0 %]	672	97 [14.5 %]	153 [22.8 %]	728#	*Time:*
GPF	656+	67 [10.1 %]	16 [2.4 %]	606+	38 [6.2 %]	13 [2.1 %]	581+	96 [16.5 %]	137 [23.6 %]	622+	MPF/GPF:X^2=60.74, p=0.0001;
SAF	67*	.	.	67*	2 [3.1 %]	2 [3.1 %]	67*	6 [9.4 %]	11 [17.2 %]	72*	All: X^2=47.56, p=0.0001.
2 (0.1 g ≤ x < 1.0 g)											*Plot type x time:*
MPF	526#	151 [28.8 %]	13 [2.5 %]	388#	49 [12.7 %]	14 [3.7 %]	354#	35 [9.8 %]	138 [39.1 %]	457	MPF/GPF:X^2=4.26, p=0.2345;
GPF	665+	212 [31.9 %]	42 [6.2 %]	494+	72 [14.5 %]	18 [3.7 %]	441+	94 [21.3 %]	177 [40.2 %]	524+	All: X^2=29.25, p=0.0001.
SAF	150*	.	.	150*	8 [5.6 %]	7 [4.9 %]	149*	24 [16.1 %]	45 [30.1 %]	170*	*Seed-mass x time:*
3 (0.001 g ≤ x < 0.1 g)											MPF/GPF:X^2=167.69, p=0.0001;
MPF	72	44 [61.6 %]	6 [7.0 %]	33	4 [10.9 %]	20 [58.7 %]	49	20 [41.2 %]	58 [118 %]	87#	All: X^2=100.78, p=0.0001.
GPF	84+	56 [67.0 %]	11 [13.0 %]	39+	9 [23.9 %]	45 [115 %]	74+	45 [61.4 %]	185 [250 %]	213	*Plot type x seed-mass x time:*
SAF	186*	.	.	186*	38 [20.1 %]	72 [38.5 %]	221*	91 [41.0 %]	72 [32.5 %]	202*	MPF/GPF:X^2=23.92, p=0.0044;
4 (x < 0.001 g)											All: X^2=90.63, p=0.0001.
MPF	41	4 [10.7 %]	1 [1.8 %]	37#	7 [19.6 %]	1 [2.0 %]	30	1 [4.8 %]	1 [4.8 %]	30	
GPF	22+	3 [15.4 %]	0	18+	3 [13.6 %]	1 [4.5 %]	17+	1 [5.0 %]	2 [10.0 %]	18+	
SAF	261*	.	.	261*	31 [12.0 %]	15 [5.6 %]	245*	68 [27.7 %]	53 [21.7 %]	230*	

occurring in significantly greater numbers in GPF than in MPF (Table 7.8). With SAF included in the G-tests, seed-group 3 still showed significant associations among plot types and time (G=116.26, p=0.001). There was also weak evidence of association for seed-group 2 species (G=14.44, p=0.025). These associations reflected the dominance of *Clinostigma* and *Campnosperma* in seed-groups 2 and 3, respectively, and the two species's high drought-induced mortality and new recruitment. Excluding *Campnosperma*, interactions of seed-group 3 frequencies among plot types over time were no longer significant (MPF + GPF G=0.499, p=0.919; all plot types G=1.37, p=0.968). Similarly, excluding *Clinostigma* from seed-group 2 removed the weak interaction among all plot types over time (G=1.36, p=0.968).

Of the ten most abundant species (see Tables 7.9a, 7.9b), only *Campnosperma* frequencies changed over time uniquely in GPF and MPF (plot type x time G=18.06, p=0.001). Among all three plot types, only the stocking of *Campnosperma* and *Clinostigma* changed significantly among the plot types (plot type x time G=175.90, p=0.001, and G=17.27, p=0.008, respectively). *Clinostigma*'s results were largely attributable to a contrast between its sharp decline in the forest plots during the drought, and no change in the few plants present in SAF.

By 15 months, *Campnosperma* occurred in significantly greater frequencies in GPF than in MPF, but it was similar between GPF and SAF (Table 7.9a). *Palaquium karrak* Kaneh. occurred in significantly greater numbers in MPF than in GPF (or SAF) (see Appendix C). This was probably an artefact of an initial stochastic effect: frequency differences for *Palaquium* were almost significant between MPF and GPF at time 0 (Gadj=5.17, p~0.025), but neither mortality nor new recruitment was significantly different. Like *Parinari, Myristica*, and, to a lesser extent, *Clinostigma*, *Palaquium* has rather large, very sticky fruits and probably limited dispersal away from the parent tree. Despite greater numbers of new recruits, there were no significant frequency differences between MPF and GPF for *Aglaia* at 15 months (Table 7.9a), or for *Syzygium* (Table 7.9b). All other species patterns present at time 0 between MPF/GPF and SAF were still evident at 15 months.

Species presence/absence among plot types changed very little over 15 months, with the exception of Vine 1 and *Paspalum conjugatum* Bergius, that lost rank in SAF (Appendix E). Ordinations of species presence at 15 months were not substantially different from assemblages illustrated at time 0 (see Chapter Six), so are not presented.

Table 7.9a Changes in stem frequencies over 15 months for common species.
% mortality is the number dead out of the previous census total (e.g., deadt0-1/ present t0). Recruitment ratio (no. new recruits/ total at previous census) is in brackets [ ] after new recruits stem frequency. # denotes a significant difference (adjusted G with p<0.01) in stem frequency between MPF and GPF, * MPF vs. SAF, and + GPF vs. SAF.

	Present T0	Dead 0-1 month	New 0-1 month	Present 1 month	Dead 1-3 mo.	New 1-3 mo.	Present 3 mo.	Dead 3-15 mo.	New 3-15 mo.	Present 15 mo.
By species:										
Parinari										
MPF	675	80 [11.8 %]	14 [2.1 %]	610	33 [5.4 %]	6 [1.0 %]	583	74 [12.7 %]	115 [19.8 %]	624
GPF	585+	53 [9.0 %]	16 [2.7 %]	548+	23 [4.1 %]	12 [2.1 %]	537+	86 [15.9 %]	113 [19.9 %]	564+
SAF	39*	.	.	39*	0	0	39*	2 [5.4 %]	4 [10.8 %]	41*
Aglaia										
MPF	222	26 [11.8 %]	4 [2.0 %]	200	11 [5.4 %]	3 [1.4 %]	192	13 [6.8 %]	54 [28.3 %]	233
GPF	262+	25 [9.6 %]	9 [3.5 %]	246+	14 [5.8 %]	6 [2.4 %]	238+	42 [17.7 %]	80 [33.6 %]	276+
SAF	99*	.	.	99*	6 [6.3 %]	6 [6.3 %]	99*	15 [14.7 %]	29 [29.5 %]	114*
Clinostigma										
MPF	203#	118 [58.2 %]	4 [2.1 %]	89#	29 [32.5 %]	8 [8.9 %]	68#	15 [22.1 %]	54 [77.9 %]	107#
GPF	329+	185 [56.1 %]	30 [9.2 %]	175+	56 [32.2 %]	11 [6.3 %]	129+	45 [35.1 %]	87 [66.9 %]	171+
SAF	30*	.	.	30*	2 [6.9 %]	1 [3.4 %]	29*	7 [25.0 %]	8 [28.6 %]	30*
Campnosperma										
MPF	44	43 [96.7 %]	4 [8.2 %]	5	3 [57.1 %]	14 [271 %]	16#	14 [86.4 %]	52 [327 %]	54#
GPF	58+	55 [95.7 %]	8 [14.5 %]	11+	8 [76.9 %]	44 [400 %]	46+	40 [87.3 %]	174 [376 %]	180
SAF	122*	.	.	122*	35 [29.1 %]	65 [53.0 %]	151*	82 [54.5 %]	69 [45.5 %]	138*
Cyathea										
MPF	28	2 [7.9 %]	0	25	6 [22.9 %]	1 [2.9 %]	20	1 [3.6 %]	1 [3.6 %]	20
GPF	20+	3 [16.7 %]	0	17+	3 [15.0 %]	0	14+	1 [5.9 %]	0	13+
SAF	113*	.	.	113*	14 [12.0 %]	10 [9.3 %]	109*	14 [12.4 %]	25 [22.9 %]	121*

Table 7.9b Changes in stem frequencies over 15 months for common species.
% mortality is the number dead out of the previous census total (e.g., deadt0-1/ present t0). Recruitment ratio (no. new recruits/ total at previous census) is in brackets [ ] after new recruits stem frequency. # denotes a significant difference (adjusted G with $p<0.01$) in stem frequency between MPF and GPF, * MPF vs. SAF, and + GPF vs. SAF.

	Present T0	Dead 0-1 month	New 0-1 month	Present 1 month	Dead 1-3 mo.	New 1-3 mo.	Present 3 mo.	Dead 3-15 mo.	New 3-15 mo.	Present 15 mo.
By species:										
Melastoma										
MPF	1	0	0	1	0	0	1	1	0	0
GPF	0+	0	0	0+	0	0	0+	0	0	0+
SAF	114*	.	.	114*	11 [10.1 %]	2 [1.8 %]	104*	46 [44.0 %]	24 [23.0 %]	82*
Myristica										
MPF	105#	20 [19.3 %]	1 [0.7 %]	86#	5 [5.9 %]	1 [1.7 %]	82#	23 [28.3 %]	38 [46.0 %]	96#
GPF	66+	13 [19.2 %]	0	53+	14 [27.0 %]	1 [1.6 %]	39+	10 [25.5 %]	24 [61.7 %]	54+
SAF	10*	.	.	10*	2 [20.0 %]	2 [20.0 %]	10*	3 [30.0 %]	6 [60.0 %]	14*
Pandanus										
MPF	20	1 [3.6 %]	0	20	0	0	20	0	2 [11.1 %]	22
GPF	31	0	1 [2.7 %]	32	0	0	32	3 [7.9 %]	1 [2.6 %]	30
SAF	18	.	.	18	0	0	18	1 [5.9 %]	7 [41.2 %]	24
Embelia										
MPF	19	1 [3.8 %]	2 [11.5 %]	20	1 [3.6 %]	6 [28.6 %]	25	7 [25.7 %]	3 [11.4 %]	22
GPF	23	1 [3.7 %]	3 [11.1 %]	24	1 [3.4 %]	1 [3.4 %]	24	5 [20.7 %]	5 [20.7 %]	24+
SAF	10	.	.	10	1 [10.0 %]	1 [10.0 %]	10	1 [11.1 %]	0	9
Syzygium										
MPF	30	4 [11.9 %]	3 [9.5 %]	30	7 [22.0 %]	2 [7.3 %]	25	4 [17.1 %]	16 [62.9 %]	37
GPF	26	2 [6.5 %]	1 [3.2 %]	25	1 [3.3 %]	1 [3.3 %]	25	3 [13.3 %]	7 [26.7 %]	29
SAF	0	.	.	0	0	0	0	0	0	0

Mortality

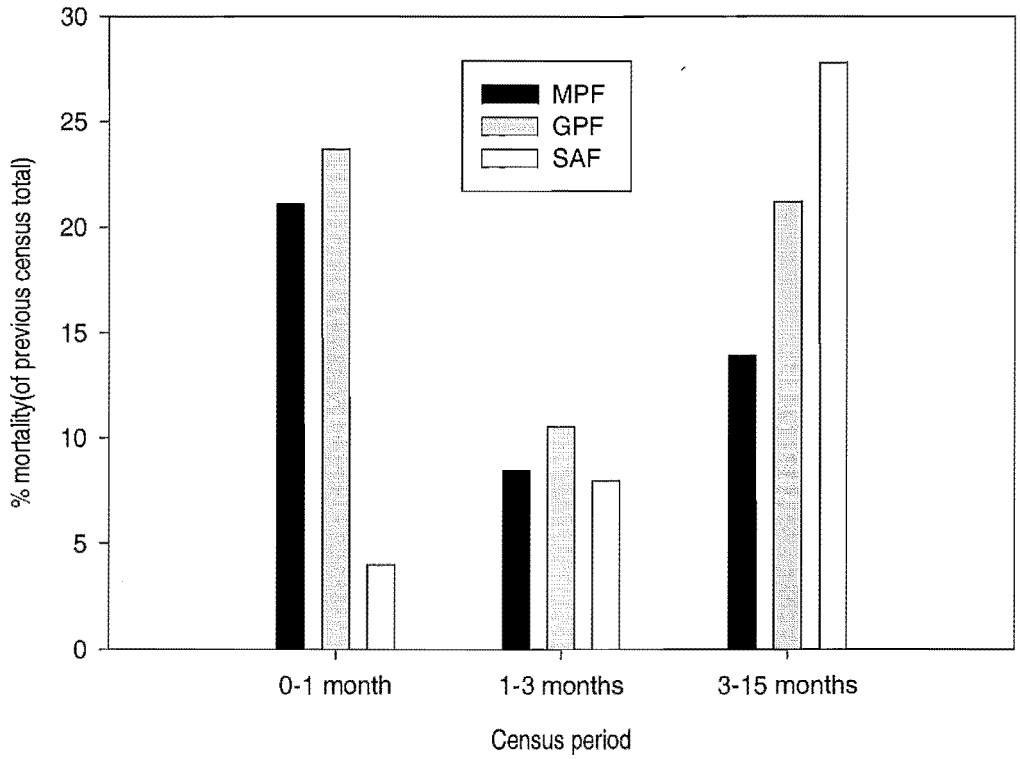

Figure 7.10 Mortality between each census, among plot types.

Although MPF and GPF stocking remained similar at each census (with the exception of *Campnosperma*), dynamics between each census were high (Figure 7.10). Mortality (as a percentage of the previous census total) was consistently greater in GPF than in MPF, especially over 3-15 months (plot type x dead/survive G= 26.55, p=0.001). Spread monthly, mortality in MPF was 21 % in the first month, 4.2 % per month through the 1-3 month period, and 1.2 % per month over the next year. Mortality for GPF was 24 % for the first month, 5.2 % per month over the 1-3 month period, and 1.8 % per month between 3 and 15 months. Assuming that mortality was similar in SAF over 0-3 months, SAF mortality was less than the forest plots during the drought periods, particularly 0-1 month (plot type x survival G=158.61, p=0.001), but greater during the regular wet periods (3-15 months plot type x survival G=61.80, p=0.001).

Mortality results mostly reflect the effects of seedlings (Table 7.6). Of total mortality per census, only 1-4 % of forest mortality was due to plants taller than 1 m height, while ~10 % of mortality in SAF was due to plants taller than 1 m. Among

life-forms, seedling mortality was significantly higher in GPF than in MPF over 3-15 months for large- and small-tree species (G=8.24, p=0.004, and G=17.51, p=0.001, respectively). Mortality was greater in MPF than GPF during 1-3 months for medium-tree species (G=7.17, p=0.007). SAF mortality was lower than both forest plot types for large- and small-tree species 0-1 months (G=33.26, p=0.001, and G=19.06, p=0.001, respectively), but higher over 3-15 months (G=80.31, p=0.001, and G=19.70, p=0.001, respectively).

By seed-mass group, seedling mortality was only significantly different between MPF and GPF for seed group 2 over 3-15 months (G=21.70, p=0.001). Even without *Clinostigma*, results were still significant (without *Clinostigma*: G=14.24, p=0.001). Among all plot types, seedling mortality in seed group 1 was significantly lower in SAF 0-1 month than in the forest plots (G=18.73, p=0.001). For seed group 2, mortality was less than 5 % in SAF versus ~35 % 0-1 month and ~17 % 1-3 months in both the forest plots (0-1 month G=71.70, p=0.001; 1-3 months G=15.42, p=0.001). During the 3-15 month period, SAF mortality rose to 18 %, GPF mortality was approximately 26 %, and MPF 13 % (G=22.00, p=0.001). Initial drought mortality among seed-group 3 seedlings 0-1 month was significantly lower in SAF (10 %) than in the forest plots (67-71 %) (G=109.57, p=0.001). However, when *Campnosperma* mortality was excluded, differences were no longer significant (G=1.86, p=0.3950).

Mortality of *Aglaia* seedlings was significantly higher in GPF 3-15 months (20 %) than in MPF (8 %) (G=15.33, p=0.001). Mortality of *Myristica* was higher in the latter period of the drought in GPF (31 %) than in MPF (7 %) (1-3 months G=15.44, p=0.001). Mortality of *Campnosperma* was much lower in SAF during the drought months than in the forest plots (e.g., 16 % mortality in SAF 0-1 month vs. ~98 % in MPF and GPF, G=152.94, p=0.001). *Aglaia* also had lower mortality in SAF 0-1 month (2 %) than in MPF (13 %) or GPF (11 %) (G=9.81, p=0.007), but over 3-15 months, the plot type rates changed (13 % mortality in SAF, 20 % in GPF, and 8 % in MPF; G=15.34, p=0.001).

Table 7.10a Percentages of the time 0 population remaining at each census, seedlings
(standardised frequencies in brackets)

	0 months	1 month	3 months	15 months
MPF	100 % (1146/1146)	74.21 % (850/1146)	66.62 % (763/1146)	56.83 % (651/1146)
GPF	100 % (1217/1217)	72.53 % (883/1217)	65.22 % (794/1217)	51.90 % (632/1217)
SAF	100 % (452/452)	.	84.10 % (380/452)	62.00 % (280/452)

Table 7.10b Percentages of the time 0 population remaining at each census, saplings 1-4 m height
(standardised frequencies in brackets)

	0 months	1 month	3 months	15 months
MPF	100 % (219/219)	98.34 % (215/219)	97.35 % (213/219)	93.71 % (205/219)
GPF	100 % (162/162)	99.48 % (161/162)	97.92 % (158/162)	94.27 % (152/162)
SAF	100 % (200/200)	.	95.83 % (192/200)	84.38 % (169/200)

A comparison of survival within just the initial time 0 population, through the census times, found that seedling survival in SAF was higher than in the forest plots (Table 7.10a), but lower for saplings (Table 7.10b). Seedling survival was consistently higher in MPF than in GPF, but sapling survival was similar. Over all plot types, mortality tended to be higher for seedlings than for saplings 1-4 m height; mortality of individuals taller than 4 m height was negligible (Table 7.6).

Within the time 0 seedling cohort and with all species combined, survivors were significantly taller at time 0 than those that died (Table 7.11). Among those that died, time to death was faster for smaller individuals. Hence, the taller the individual, the greater was its chance of survival. However, although not significant, initial heights of *Aglaia*, *Clinostigma*, and *Campnosperma* plants that died by 3 months were slightly taller than the ones that died by 15 months. The severity of the drought on these species probably meant that even larger seedlings were killed during the first three months, whereas the larger advance-growth seedling height of *Parinari* enabled all but its shortest seedlings to survive the drought. The cohort effects were independent of plot-type. There were no significant interactions of plot type by cohort when all species were combined ($F=0.32$, $p=0.8968$), nor for any life-form, seed-mass group, or common species when analysed separately.

Table 7.11 Mean height (m) at time 0 vs. length of time survived, for seedlings (≤ 1 m height). Means with the same letter are not significantly different in an LSD test with α=0.01.

	Died by 1 month	Died by 3 months	Died by 15 months	Survived 15 months
All species combined:	0.19 ± 0.03 c	0.28 ± 0.02 bc	0.34 ± 0.02 b	0.44 ± 0.02 a
Life-form:				
Large-tree species	0.21 ± 0.02 c	0.34 ± 0.04 b	0.40 ± 0.04 b	0.57 ± 0.03 a
Medium tree spp.	0.12 ± 0.02 a	0.23 ± 0.07 a	0.12 ± 0.01 a	0.26 ± 0.03 a
Small-tree spp.	0.09 ± 0.01 b	0.12 ± 0.01 b	0.14 ± 0.02 b	0.28 ± 0.02 a
Shrub spp.	0.14 ± 0.07 a	0.15 ± 0.04 a	0.15 ± 0.04 a	0.32 ± 0.05 a
Seed-mass group:				
1 (x ≥ 1.0 g)	0.41 ± 0.03 b	0.49 ± 0.03 ab	0.52 ± 0.04 ab	0.60 ± 0.02 a
2 (0.1 g ≤ x < 1.0 g)	0.11 ± 0.01 b	0.14 ± 0.02 b	0.14 ± 0.02 b	0.27 ± 0.02 a
3 (0.001 g ≤ x < 0.1 g)	0.06 ± 0.00 b	0.25 ± 0.09 a	0.13 ± 0.04 ab	0.27 ± 0.03 a
4 (x < 0.001 g)	0.10 ± 0.04 b	0.13 ± 0.03 b	0.21 ± 0.05 ab	0.36 ± 0.03 a
Species:				
Parinari	0.43 ± 0.03 c	0.55 ± 0.02 b	0.60 ± 0.04 ab	0.65 ± 0.01 a
Aglaia	0.09 ± 0.01 b	0.12 ± 0.02 b	0.11 ± 0.01 b	0.23 ± 0.02 a
Clinostigma	0.11 ± 0.01 b	0.17 ± 0.03 b	0.14 ± 0.02 b	0.44 ± 0.08 a
Campnosperma	0.06 ± 0.00 b	0.25 ± 0.11 ab	0.18 ± 0.07 ab	0.47 ± 0.17 a

Over the 3-15 month, post-drought year, seedling survival for a particular cohort tended to be greatest in MPF and least in SAF, and older individuals showed greater survival than newer recruits (Table 7.12). Note that as there were no significant plot-type interactions with survival and cohort for any of the species sub-groups in Table 7.12, data from all three plot types were pooled and these pooled ratios of survival vs. death were analysed among the recruitment cohorts. The greatest survival differences among the cohorts were mostly between those present at time 0 or recruited by one month, and three-month recruits. In species that have large advance growth, for example, *Parinari*, the weakest plants have probably already died before three months so individuals in the older cohorts are more durable than the most recently recruited individuals. Overall, survival of *Parinari* and *Aglaia* seedlings was considerable higher than *Clinostigma* and *Campnosperma*.

Table 7.12 Survival of seedlings of each time-recruited cohort during the 3-15 month period
(i.e., the number alive at 15 months / number alive at 3 months).
* denotes a significant G-test interaction of pooled survival vs. recruitment cohorts with $p < 0.01$.

	Mature-phase forest			**Gap-phase forest**			**Sakau-agro forest**	
Cohort:	Present time 0	1 mo. recruits	3 mo. recruits	Present time 0	1 mo. recruits	3 mo. recruits	Present time 0	3 mo. recruits
All species combined: *	84.87 % (642/756)	77.78 % (20/26)	31.48 % (12/39)	79.73 % (638/800)	64.44 % (24/37)	28.57 % (22/77)	72.16 % (265/367)	27.78 % (26/94)
Life-form:								
Large-tree species *	80.73 % (401/497)	81.82 % (13/16)	18.92 % (5/27)	77.58 % (404/521)	65.63 % (18/27)	24.69 % (17/68)	65.79 % (52/79)	6.25 % (4/67)
Small-tree spp.	93.98 % (181/193)	66.67 % (3/4)	75.0 % (2/3)	82.20 % (182/221)	77.78 % (6/8)	62.50 % (4/7)	82.74 % (170/205)	86.36 % (20/23)
Seed-mass group:								
1 ($x \geq 1.0$ g)	81.98 % (389/475)	85.71 % (13/15)	50.0 % (4/8)	80.96 % (368/455)	83.33 % (13/16)	73.33 % (9/12)	92.68 % (40/43)	0 (0/2)
2 (0.1 g $\leq x <$ 1.0 g) *	89.91 % (220/245)	63.64 % (5/8)	41.18 % (5/12)	76.68 % (240/313)	56.52 % (18/19)	40.91 % (8/19)	83.0 % (86/104)	66.67 % (4/6)
3 (0.001 g $\leq x <$ 0.1g) *	82.14 % (17/21)	75.0 % (2/3)	18.52 % (4/20)	88.46 % (19/22)	25.0 % (1/4)	9.43 % (4/44)	69.62 % (57/82)	15.94 % (11/71)
4 ($x <$ 0.001 g)	95.83 % (17/18)	.	.	100 % (10/10)	.	(1)	59.09 % (81/137)	76.92 % (10/13)
Species:								
Parinari	84.11 % (341/405)	85.0 % (12/14)	50.0 % (3/6)	81.67 % (345/422)	83.33 % (13/16)	78.57 % (9/12)	95.24 % (21/22)	.
Aglaia	93.39 % (154/165)	66.67 % (3/4)	75.0 % (2/3)	81.28 % (161/198)	75.0 % (5/7)	57.14 % (3/6)	88.31 % (71/80)	66.67 % (4/6)
Clinostigma	55.17 % (12/21)	.	0 (0/6)	54.43 % (36/66)	46.15 % (5/11)	23.08 % (3/11)	53.85 % (7/13)	.
Campnosperma	0 (0/1)	0 (0/1)	10.53 % (1/13)	0	0 (0/1)	9.62 % (4/43)	46.88 % (16/34)	6.45 % (4/64)

New recruitment

Absolute numbers of new recruits, including seedlings plus some saplings new to the four-metre square in SAF (see saplings in Table 7.6) were higher in GPF than in MPF at each census (Figure 7.11). However, patterns of change over time were similar (plot-type x time: MPF vs. GPF F=4.04, p=0.1326). New recruitment over 15 months in SAF was different from MPF and GPF (plot type x time, all F=77.55, p=0.0001).

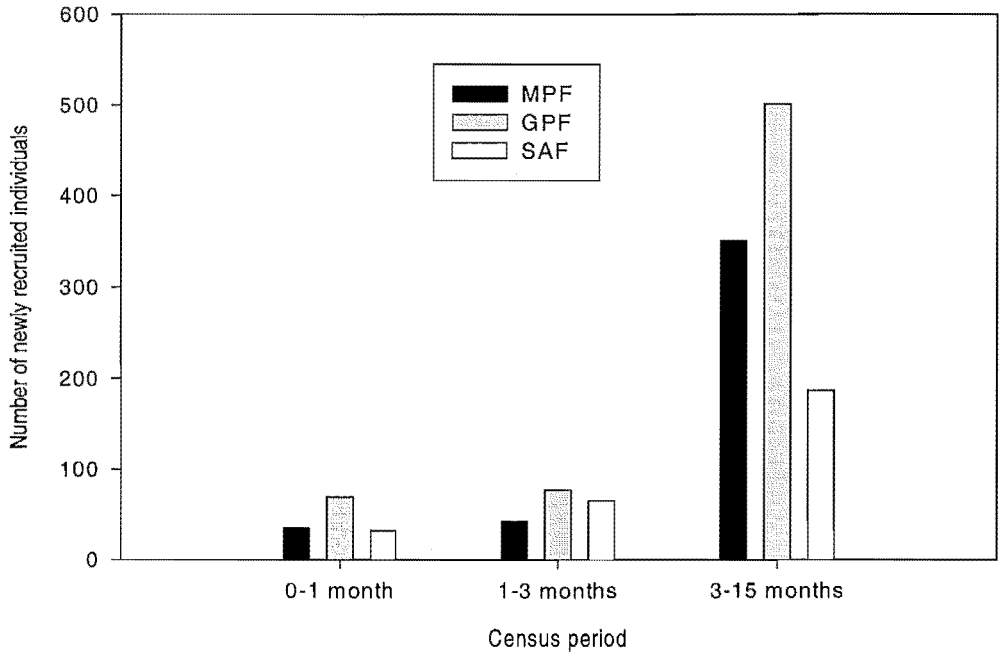

Figure 7.11 New recruitment between censuses and among plot types.

Comparing the total new recruitment per species in each plot type over the 15 months (Table 7.13), *Cyathea* and *Melastoma* were recruited into SAF in significantly greater frequencies than into MPF or GPF. *Aglaia* and *Campnosperma* regenerated in significantly greater numbers in GPF ahead of SAF or MPF. Note that neither *Campnosperma* nor *Aglaia* was significantly different in presence/absence or stem frequencies at time 0 between GPF and MPF. Nevertheless, *Campnosperma* formed a greater proportion of all newly recruited seedlings in SAF (60 %) than in GPF (35 %) or MPF (16 %) (Appendix D). *Clinostigma* also regenerated in significantly greater numbers in GPF than MPF. However, this may be related to the patchy occurrence of *Clinostigma* shown in the initial time 0 frequency differences between MPF and GPF, rather than a preference by this species for the GPF environment. *Parinari*, *Clinostigma*, *Aglaia*, and *Myristica* were all recruited in significantly greater numbers

in both MPF and GPF ahead of SAF. Note that when the most common species in each seed-mass group, (i.e., *Parinari*, SD1; *Clinostigma*, SD2; *Campnosperma*, SD3; and *Cyathea*, SD4) were excluded, MPF and GPF were no longer significantly different; apart from group 3, differences between MPF or GPF, and SAF remained.

Table 7.13 Total new recruits in 15 months and associated G-tests.
New recruits totals were summed from all censuses after time 0 and standardised to 100-quadrat equal areas. Paired G-test (adjusted) comparisons are given in the order MPF vs. GPF, MPF vs. SAF, and GPF vs. SAF, respectively. * indicates that the Gadj-statistic is significant at $p<0.01$. Note: numbers less than 5 were changed to 5 in the G-tests for improving test validity.

	MPF	GPF	SAF	Gadj-test statistics
All species combined:	428	646	282	Gadj: MPF vs. GPF=44.54*, MPF vs. SAF= 30.22*, GPF vs. SAF= 146.60*
By life-form:				
Large-tree spp.	312	521	155	Gadj=52.97*, 53.77*, 209.04*
Medium-tree spp.	32	11	0	Gadj=10.59*, 21.69*, 2.24
Small-tree spp.	70	105	95	Gadj=7.03*, 3.79, 0.50
Shrub spp.	14	9	32	Gadj=1.07, 7.16*, 13.52*
By seed-mass group:				
1 ($x \geq 1.0$ g)	175	166	14	Gadj=0.24, 161.77*, 150.72*
2 (0.1 g $\leq x <$ 1.0 g)	166	237	52	Gadj=12.56*, 62.54*, 128.01*
3 (0.001 g $\leq x <$ 0.1g)	83	240	144	Gadj=79.52*, 16.56*, 24.22*
4 ($x <$ 0.001 g)	3	3	73	Gadj=0.00, 70.53*, 70.53*
By species:				
Parinari	136	140	4	Gadj=0.06, 151.72*, 156.97*
Aglaia	62	95	35	Gadj=6.97*, 7.58*, 28.66*
Clinostigma	66	128	9	Gadj=20.11*, 48.61*, 123.07*
Campnosperma	70	226	133	Gadj=86.38*, 19.83*, 24.33*
Cyathea	1	0	35	Gadj=0.00, 25.00*, 25.00*
Melastoma	0	0	26	Gadj=0.00, 15.34*, 15.34*
Myristica	40	25	8	Gadj=3.47, 23.05*, 9.06*
Embelia	11	8	1	Gadj=0.46, 2.24, 0.67
Syzygium	21	8	0	Gadj=5.94, 10.39*, 0.67
Palaquium	9	3	0	Gadj=1.12, 1.12, 0.00

An ordination of the total new recruitment over 15 months per species in each MPF and GPF quadrat spaced species along a weak light gradient over axis 1 (Figure 7.12, Spearman's correlation coefficient: axis 1 vs. ISFC =0.3844, n=75), but none of the measured variables was even weakly correlated with axis 2.

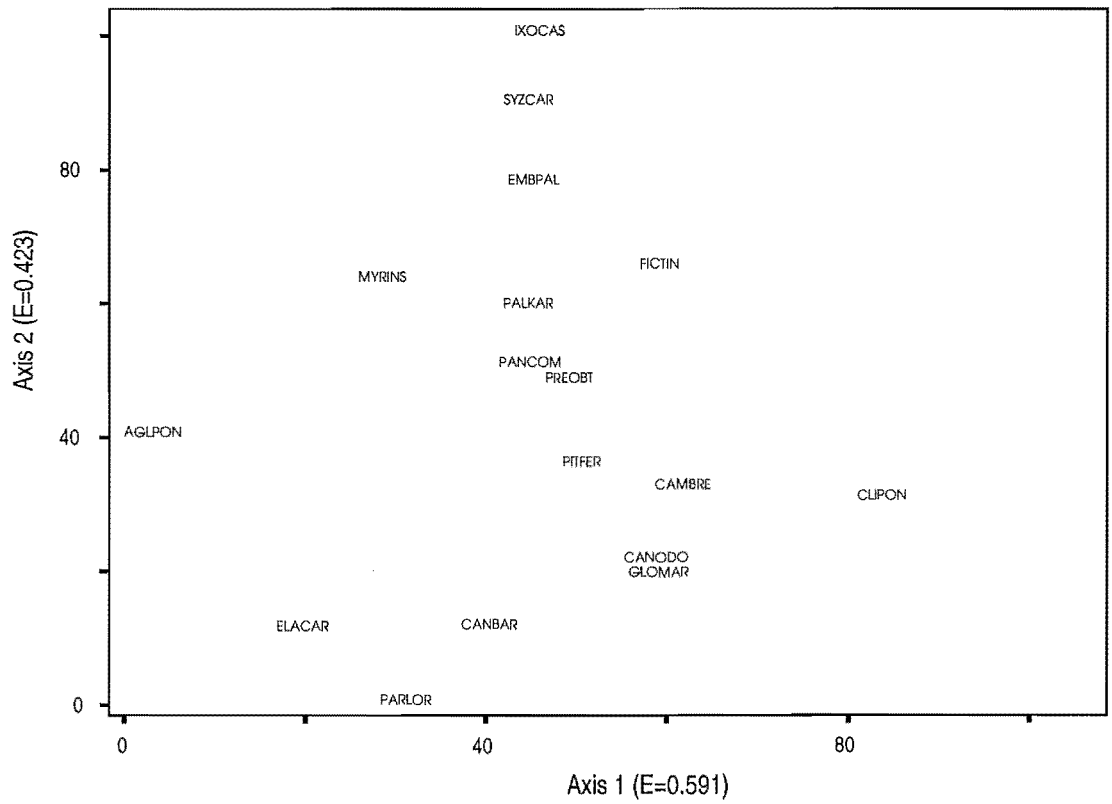

Figure 7.12a DCA: Species total new recruitment in quadrats, MPF and GPF only.
Species abbreviations use the first three letters of the genus then species.

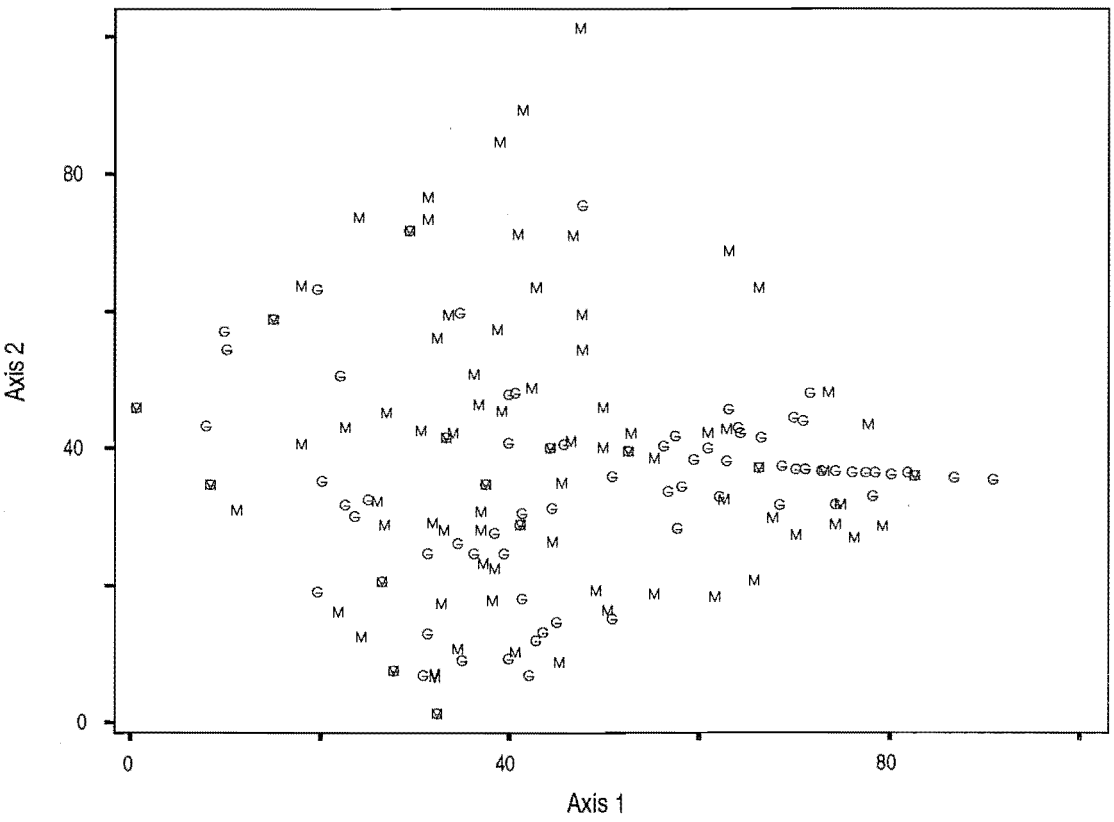

Figure 7.12b DCA: Distribution of quadrats from ordination of species new recruitment.
M=MPF, G=GPF.

Correlations against light, litter, and non-woody cover found only total quadrat new recruitment of seed-group 3, *Clinostigma*, and *Campnosperma* (dominates seed-group 3) were correlated with any variable (photo-papers at 1 m (n=40): R=0.4929, p=0.0012; R=0.5101, p=0.0008; and R=0.4795, p=0.0017 respectively). For MPF and GPF plot totals of new recruits (square-root transformed) vs. canopy openness, litter volume, and non-woody cover, only the following relationships were found (analysed with ANOVA, n=13 plots):

- All species vs. canopy openness: F=10.20, p=0.0086, R^2=48.11 %;
- Seed-group 2 vs. canopy openness: F=7.29, p=0.0207, R^2=39.85 %;
- Seed-group 4 vs. litter volume at 15 months: F=8.12, p=0.0158, R^2=42.48 %.

There were no significant interactions (i.e., near p=0.01) or other main effects.

For all quadrats combined (i.e., SAF included), the first two ordination axes arranged species in quadrat space partly along a light gradient (Figure 7.13a, b), although the correlations were very weak (Axis 1 vs. ISFC (n=88): R=0.3691, Axis 2 vs. ISFC: R=0.3372; correlations with canopy openness were similar). Among individual seed groups and species, seed groups 1 and 2 showed the greatest association with quadrat light (Table 7.14). Note that plot-level ANOVA of light, litter and non-woody cover interactions were not done with all plot types combined because non-woody cover confounds SAF.

Table 7.14 Total new recruitment per quadrat vs. light measures.
Probabilities are presented only for coefficients > 0.4500.

	ISFC (n=116)	**DSFC** (n=116)	**Photo papers1 m** (n=59)	**% canopy openness** (n=353)
All species	R=-0.5086, p=0.0001	R=-0.4922, p=0.0001	R=-0.3717	R=-0.1410
Seed-group 1	R=-0.4869, p=0.0001	R=-0.4389	R=-0.4345	R=-0.3091
Seed-group 2	R=-0.5223, p=0.0001	R=-0.4987, p=0.0001	R=-0.3654	R=-0.2095
Seed-group 3	R=-0.1031	R=-0.1238	R=-0.0644	R=0.1717
Seed-group 4	R=0.3174	R=0.2629	R=0.4448	R=0.2003
Parinari	R=-0.4582, p=0.0001	R=-0.4086	R=-0.3924	R=-0.2706
Aglaia	R=-0.3513	R=-0.3205	R=-0.4283	R=-0.1488
Clinostigma	R=-0.3014	R=-0.2965	R=-0.0329	R=-0.0358
Campnosperma	R=-0.0982	R=-0.124	R=-0.0416	R=0.2031

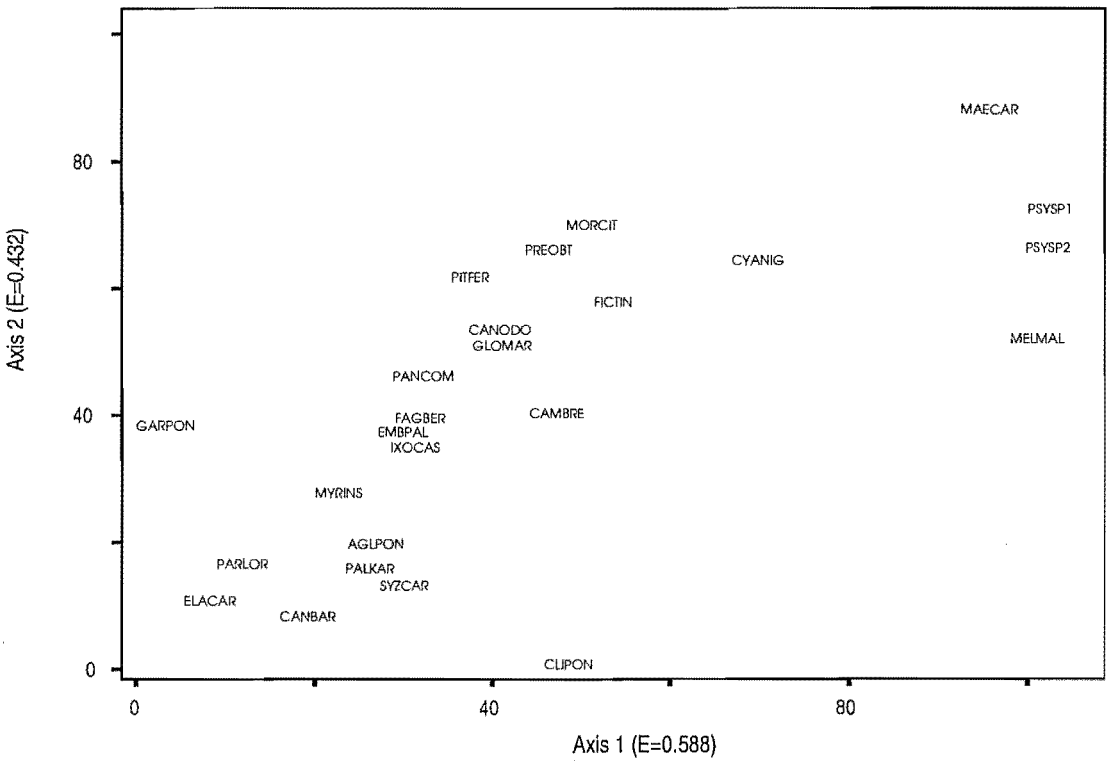

Figure 7.13a DCA: Species total new recruitment in quadrats, all plot types.
Species abbreviations use the first three letters of the genus then species.

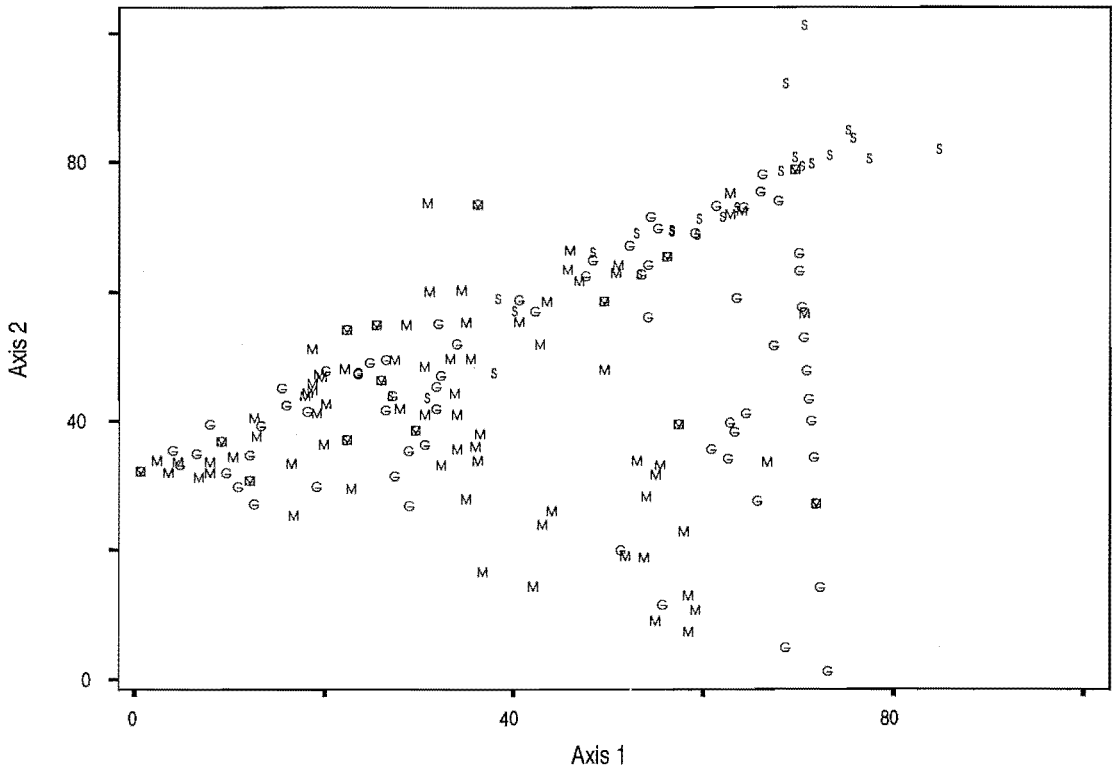

Figure 7.13b DCA: Distribution of quadrats from ordination of species new recruitment.
M=MPF, G=GPF, S=SAF.

New recruits vs. time 0 cohort at 15 months

At the final census after 15 months, seedling populations were composed of the following proportions of recruitment cohorts (Table 7.15):

Table 7.15 Representation by each recruitment cohort of the total seedling population at 15 months.
Standardised frequencies are in brackets.

	T0 cohort	1 month recruits	3-month recruits	15-month recruits
MPF	62.70 % [642/1023]	1.98 % [20]	1.20 % [12]	34.11 % [349]
GPF	53.68 % [632/1178]	2.00 % [24]	1.78 % [21]	42.54 % [501]
SAF	62.22 % [239/384]	.	5.43 % [21]	32.34 % [124]

When the new recruits were totalled and compared with seedlings that were present at time 0 and survived to 15 months, the ratio of the time 0 cohort to new recruits differed among plot types and species sub-groups. Note that the time 0 cohort is the sum of individuals potentially recruited over many years, whereas "new recruits" are those recruited over the last 15 months only.

Table 7.16 Time 0 seedlings vs. total new recruits present at 15 months, by seed-mass group.
Standardised frequencies are in brackets.

	MPF		GPF		SAF	
	T0	NR	T0	NR	T0	NR
1 ($x \geq 1.0$ g)	69.65 % [389]	30.35 % [170]	70.13 % [369]	29.87 % [157]	79.55 % [36]	20.45 % [9]
2 (0.1 g $\leq x <$ 1.0 g)	59.88 % [220]	40.12 % [147]	54.42 % [233]	45.58 % [195]	70.54 % [82]	29.46 % [34]
3 (0.001 g $\leq x <$ 0.1g)	20.72 % [17]	79.28 % [64]	9.24 % [19]	90.76 % [190]	40.15 % [55]	59.85 % [82]
4 ($x <$ 0.001 g)	92.00 % [17]	8.00 % [1]	76.47 % [11]	23.53 % [3]	77.50 % [65]	22.50 % [19]

Grouped by seed-mass, cohort ratios among seed-groups differed uniquely among plot-types (plot-type x seed-group x cohort: MPF vs. GPF, $x^2=116.53$, $p<0.0001$; all: $x^2=120.79$, $p<0.0001$) (Table 7.16). With the exception of seed group 4 (the lightest-seeded species), the ratio of new recruits vs. time 0 cohort for each seed-mass group increased with decreasing seed mass; that is, species with heavier seeds had a greater proportion of plants in the time 0 cohort than in new recruits.

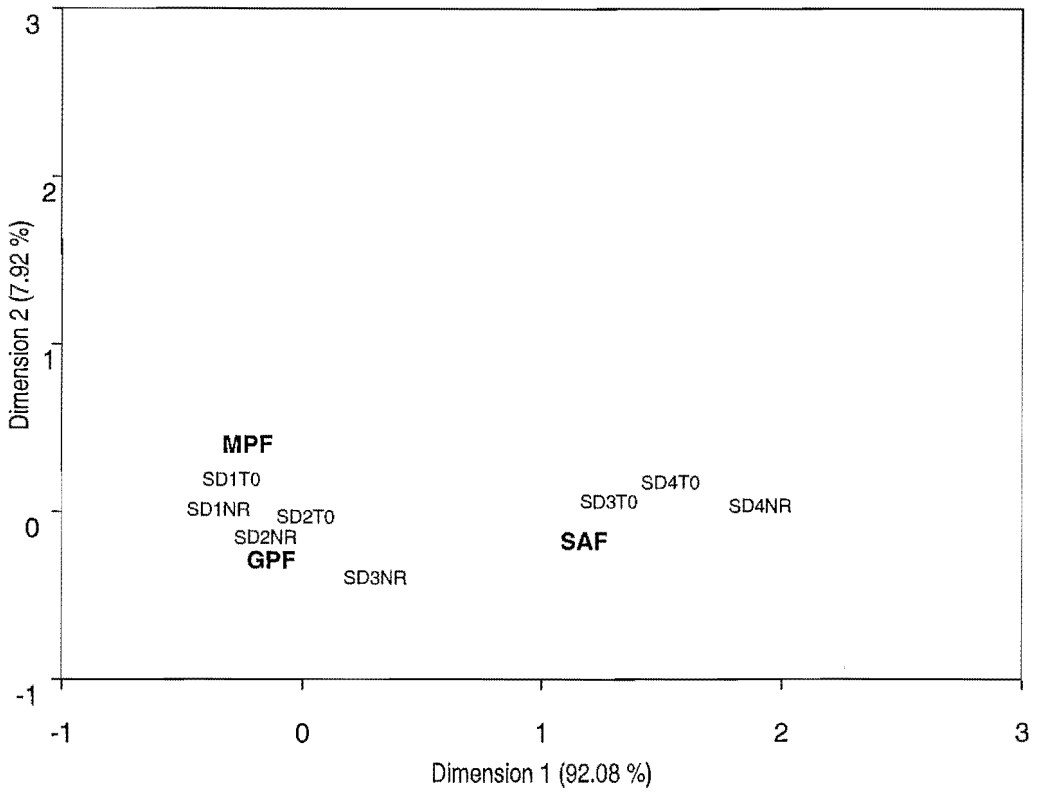

Figure 7.14 CA: Time 0 seedlings vs. total new recruits present at 15 months, by seed-mass group.

For both time 0 seedlings and newly recruited seedlings, seed groups 1 and 2 were more closely associated with MPF and GPF, and group 4 (those with the lightest seeds) was more associated with SAF (Figure 7.14). Even with the most common species in each seed-group excluded, the correspondence analysis results have the same pattern. The time 0 cohort of seed group 3 (dominated by *Campnosperma*) was more associated with SAF than the forest plot-types, but the new recruits were more associated with GPF.

These results show that the dominant contrasts already apparent between MPF and SAF at time 0, with respect to all seed-groups except group 3, were similar for individuals newly recruited over 15 months. In SAF, however, the ratio of new recruits to time 0 seedlings was lower for seed groups 1 and 2 than in the forest plots so new recruits were not successfully recruiting in SAF at the same rate as in the forest plots.

New recruitment following fire:

Between the one- and three-month re-censuses, a fire burnt half a GPF plot. Although recruitment in the few months before the fire was scant due to the drought, a

few seedlings each of *Parinari*, *Clinostigma*, and *Palaquium* were recorded. In contrast, recruitment in the severely burnt quadrats after the fire (3-15 months) included (in order of greatest abundance): *Campnosperma*, *Clinostigma*, *Pittosporum ferrugineum* W.T.Aiton, *Premna obtusifolia* R.Br., *Claoxylon carolinianum* Pax & Hoffman, *Melastoma*, *Parinari*, and a few seedlings each of *Cananga odorata* (Lam.) Hook.f. & Thomson, *Glochidion marianum* Mull.Arg., *Canthium barbatum* (G.Forst.) Seem., *Palaquium*, *Embelia palauensis* Mez, *Aglaia*, and *Ficus tinctoria* G.Forst. *Eragrostis* grass and the ferns *Nephrolepis* and *Sphaerostephanos* became newly established in a few quadrats. Many of these species were previously uncommon or absent from this plot (and other forest plots), but were common in SAF plots. *Parinari* and *Clinostigma* were still recruited after the fire but were most abundant in the quadrats that were not burnt.

7.2.2 Health, (0-3 months)

By 3 months, overall there was still a higher proportion of healthy seedlings and saplings in SAF than in MPF or GPF (Table 7.17). In the forest plots, GPF contained a significantly lower proportion of healthy seedlings than MPF because there were more physically damaged plants in GPF following gap openings.

Among life-forms and seed-mass groups, a greater but not significant proportion of seedlings from small-tree species were classed as healthy in MPF and SAF than in GPF (MPF vs. GPF $G=5.40$, $p=0.02$; all $G_{adj}=8.88$, $p<0.02$). Also, seed-group 1 decreased more in % health in GPF than MPF (or SAF) (MPF vs. GPF time 2 $G=9.22$, $p=0.002$), particularly in the physically damaged and bent code (up from ~24 % to 31 %, c.f., 20 % up to 24 % in MPF).

At three months, *Campnosperma* health was no longer significantly lower in SAF than in MPF or GPF (all $G=4.86$, $p=0.088$, c.f., time 0 $G=22.24$, $p=0.01$). SAF health increased because as some *Campnosperma* seedlings died in the drought and many new recruits arrived, the population appeared healthier at time 2, in much the same way as the almost 100 % seedling mortality rate in GPF and MPF leaves only new (healthy) recruits at the next census. *Clinostigma* health decreased in both MPF and GPF over three months, but MPF health dropped considerably more (MPF time 0: 80 %, time 2: 66 %, c.f., GPF time 0: 72 %, time 2: 68 %). Mortality of *Parinari* during the drought was lower than for *Clinostigma* or *Campnosperma* so as *Parinari* persisted, they became less healthy, and in particular more bent.

In MPF and GPF, of those physically damaged by debris, the most commonly recorded debris-types were *Clinostigma* fronds or inflorescences (~ 60 % of all recordings), branches (increasing in GPF after gap openings up to 27 % from 7 %), or neighbouring plants.

Table 7.17 Health of a) Seedlings ≤ 1.0 m height and, b) saplings 1-4 m height, at 0 and 3 months.
Percentages are derived from raw frequencies, but frequencies shown in brackets [ ] have been standardised to equal areas. For G-test statistics, * denotes a significant test result at $p \leq 0.01$.

	Time 0			Three months			G-test
	MPF	GPF	SAF	MPF	GPF	SAF	Statistics
A. Seedlings ≤ 1.0 m height							Healthy vs. not-healthy: Time 0,
% health [#]	73.45 %	70.65 %	80.32 %	69.31 %	64.12 %	81.35 %	MPF vs. GPF G=2.95, MPFp vs.
	[842/1146]	[860/1217]	[366/455]	[570/822]	[586/913]	[377/464]	SAF G=13.86*; time 2: MPF vs.
% physical damage & bent [#]	16.37 % [188]	18.65 % [227]	10.76 % [49]	19.66 % [162]	22.45 % [205]	10.11 % [47]	GPF G=6.74*, all G=46.64*.
% physical damage - not bent [#]	3.16 % [36]	4.70 % [57]	6.86 % [31]	3.26 % [27]	6.53 % [60]	5.84 % [27]	Proportions among non-health
% biotic coverage [#]	7.02 % [80]	5.73 % [70]	0.69 % [3]	6.17 % [51]	5.15 % [47]	0.45 % [2]	codes: T0, MPF vs. GPF G=7.04,
% drought-stressed [#]	0.0		1.37 % [6]	1.59 % [13]	1.75 % [16]	2.25 % [10]	MPFp vs. SAF G=31.97*; T2: MPF
							vs. GPF G=11.03*, all G=34.66*.
B. Saplings 1-4 m height							Healthy vs. not-healthy: Time 0,
% health [#]	66.89 %	63.16 %	84.21 %	67.65 %	61.49 %	85.71 %	MPF vs. GPF G=0.72, MPFp vs.
	[146/219]	[101/160]	[167/198]	[150/222]	[90/146]	[175/204]	SAF G=25.21*; time 2: MPF vs.
% physical damage & bent [#]	6.62 % [15]	7.37 % [12]	10.53 % [21]	6.21 % [14]	10.92 % [16]	9.18 % [19]	GPF G=1.84, all G=32.47*.
% physical damage - not bent [#]	2.32 % [5]	3.68 % [6]	1.58 % [3]	2.29 % [5]	4.02 % [6]	2.04 % [4]	Proportions among non-health
% biotic coverage [#]	24.17 % [53]	25.79 % [41]	1.58 % [3]	23.53 % [52]	22.99 % [34]	1.02 % [2]	codes: T0, MPF vs. GPF G=0.49,
% drought-stressed [#]	0.0	0.0	2.11 % [4]	0.33 % [1]	0.57 % [1]	2.04 % [4]	MPFp vs. SAF G=33.85*; T2: MPF
							vs. GPF G=3.35, all G=32.34*.

Health and seedling survival

Overall, surviving seedlings were significantly healthier at time 0 than those that died over the 15 months (Table 7.18). The main exception was *Campnosperma* because most of its seedlings died while they were still very small and young after initially being classed as healthy.

Table 7.18 Health status at time 0 vs. seedling survival over 15 months.
Rows add to 100 %. G-statistics tested for an interaction between the number of healthy and not healthy (biotic and physical-damage codes) seedlings, and their survival. Frequencies are standardised to 100 quadrats.

	Healthy	Biotic cover	Phys. damage - not bent	Phys. damage - bent	Total freq.	G-test statistics
All species: Died over 15mo	68.53 %	6.24 %	4.88 %	20.35 %	1538	G(health/survival)
Survived 15 mo.	77.23 %	5.26 %	3.80 %	13.71 %	1919	=32.90, p=0.001
Seed-group 1: Died	53.22 %	13.64 %	5.11 %	28.03 %	528	G=58.13, p=0.001
Survived 15 mo.	72.75 %	6.96 %	2.55 %	17.75 %	1020	
Seed-group 2: Died	71.31 %	3.20 %	5.15 %	20.33 %	718	G=29.14, p=0.001
Survived 15 mo.	83.38 %	4.01 %	4.01 %	8.61 %	674	
Seed-group 3: Died	90.05 %	0.52 %	3.66 %	5.76 %	191	G=9.85, p=0.002
Survived 15 mo.	76.19 %	2.86 %	10.48 %	10.48 %	105	
Seed-group 4: Died	88.12 %	0	3.96 %	7.92 %	101	G=1.78, p=0.182
Survived 15 mo.	81.67 %	0	7.50 %	10.83 %	120	
Parinari: Died	52.87 %	12.44 %	4.55 %	30.14 %	418	G=55.41, p=0.001
Survived 15 mo.	73.79 %	5.84 %	1.98 %	18.39 %	908	
Aglaia: Died	63.47 %	2.99 %	6.59 %	26.95 %	167	G=30.10, p=0.001
Survived 15 mo.	84.43 %	4.48 %	3.41 %	7.68 %	469	
Clinostigma: Died	74.56 %	3.52 %	4.70 %	17.22 %	511	G=0.90, p=0.343
Survived 15 mo.	79.71 %	1.45 %	10.14 %	8.70 %	69	
Campnosperma: Died	92.98 %	0	1.75 %	5.26 %	171	G=6.63, p=0.010
Survived 15 mo.	70.59 %	0	0	29.41 %	17	

Health and height growth

Table 7.19 Health status at time 0 vs. absolute height growth 0-15 months.
Results were pooled among plot types because there were no significant third-order interactions among plot type x health status x growth.

	Absolute height growth 0-15 months:		
Seedlings, all species:	**Negative / no growth**	**Positive growth**	**G-statistics**
Of those healthy at time 0:	36.26 % [532/1467]	63.74 % [935/1467]	G (Health vs.
Of those unhealthy at time 0:	41.36 % [189/457]	58.64 % [268/457]	Growth)=3.82, p=0.051
Saplings, all species:			
Of those healthy at time 0:	36.40 % [103/283]	63.60 % [180/283]	G=5.36, p=0.021
Of those unhealthy at time 0:	49.51 % [51/103]	50.49 % [52/103]	
Seedlings, *Parinari*:			
Of those healthy at time 0:	39.31 % [263/669]	60.69 % [406/669]	G=3.73, p=0.054
Of those unhealthy at time 0:	46.47 % [112/241]	53.53 % [129/241]	

Seedlings and (especially) saplings classed as healthy at time 0 tended to show more positive height growth over 0-15 months than plants initially classed as not healthy (Table 7.19). However, the weakness of interactions meant that no Spearman's correlation or linear regression between height growth (absolute or proportional) and light (indirect site factor) was improved by using healthy individuals only rather than the full dataset.

7.2.3 Height growth

Most of the changes in mean net height (averaged by plot to each plot type) occurred in the twelve months between time 2 and time 3 re-censuses following the end of the El Niño drought. No significant height differences were found among the plot types at any census for seedlings (Figure 7.15a), but for saplings (1-4 m height) SAF was significantly taller in net height from the forest plots at 15 months (Figure 7.15b, ANOVA 15 months, F=6.77, p=0.0080). Analyses with only individuals that survived from 0-15 months produced very similar results to analyses using all plants at each census (net height).

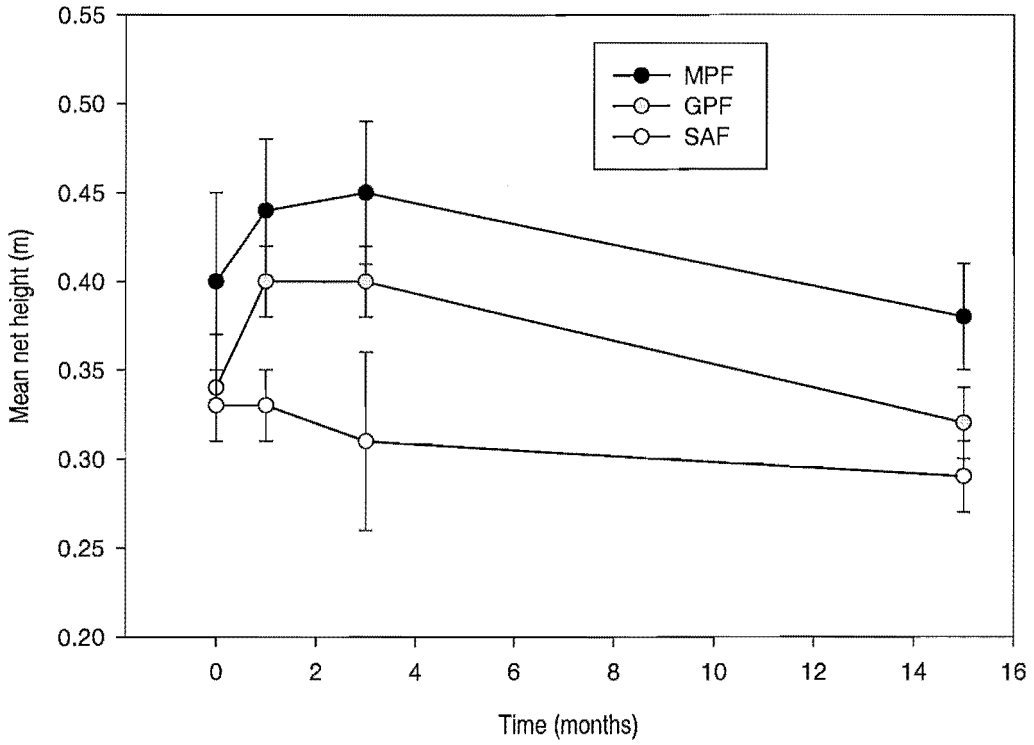

Figure 7.15a Mean net height (± standard error) per plot type over 15 months, for seedlings.

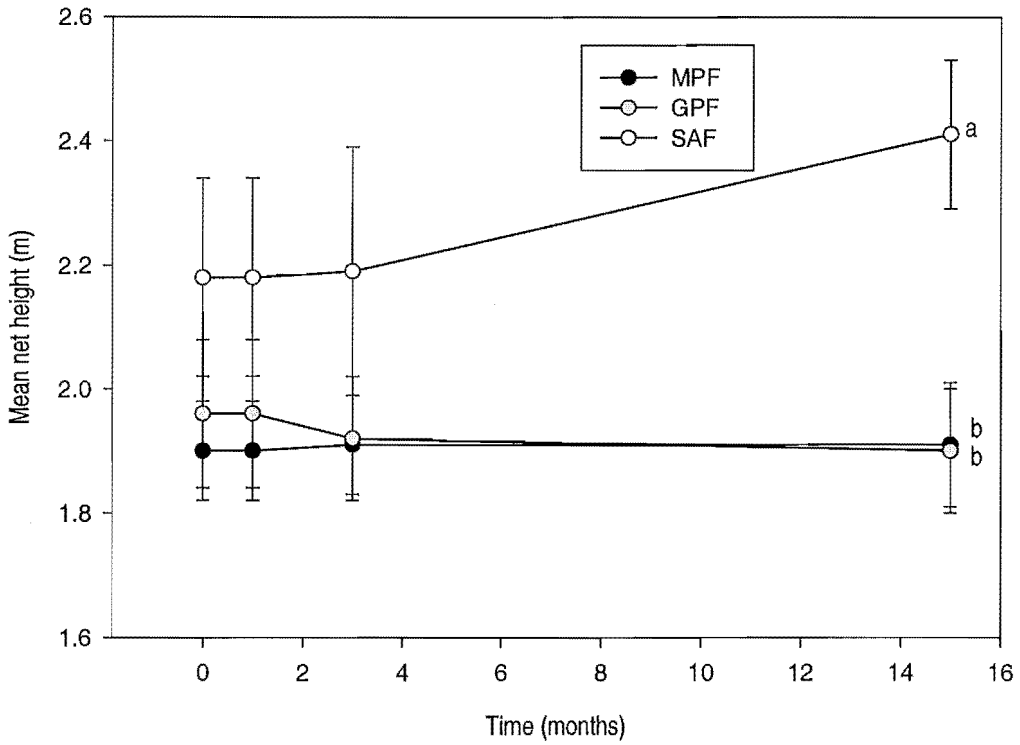

Figure 7.15b Mean net height (± standard error) per plot type over 15 months, for saplings 1-4 m height.
Means with different letters are significantly different in an LSD test with α=0.01.

Comparing proportional height-growth rates for survivors alone (Table 7.20), plants in SAF grew more than in MPF or GPF at all size-classes, but variation within plot types was high.

Table 7.20 Proportional height growth 0-15 months among plot types by size-class.
Means with different letters are significantly different in an LSD test with α=0.01.

	MPF	GPF	SAF	ANOVA test statistics
All seedlings	0.08 ± 0.02 a	0.20 ± 0.05 ab	0.56 ± 0.18 b	MPF vs. GPF: F=5.01, p=0.0468
(≤ 1.0 m height)				All: F=6.62, p=0.0087
All saplings	0.01 ± 0.01 a	0.03 ± 0.03 a	0.35 ± 0.08 b	MPF vs. GPF: F=0.39, p=0.5448
(1-4 m height)				All: F=18.42, p=0.0001
All large saplings	0.01 ± 0.02	0.04 ± 0.01	0.11 ± 0.09	MPF vs. GPF: F=0.92, p=0.3598
(4-10 m height)				All: F=0.90, p=0.4307

Among sub-groups, the most notable trends in proportional height growth among surviving seedlings (Table 7.21) were that proportional growth tended to be higher in GPF than in MPF in all sub-groups, and was significantly greater in GPF than in MPF for small-tree and shrub-species, and seed-mass group 2 species.

Table 7.21 Proportional height growth 0-15 months among plot types for seedlings ≤ 1.0 m height, by species sub-groups.
Means with different letters are significantly different in an LSD test with α=0.01.
Note: Absolute and proportional seedling height growth 0-3 months and 3-15 months among plot types and species sub-groups are presented in Appendix F.

	MPF	GPF	SAF	ANOVA test statistics
Life-form:				
Large (and medium)-tree species	0.06 ± 0.02	0.20 ± 0.08	0.23 ± 0.10	MPF vs. GPF: F=3.45, p=0.0901 All: F=1.95, p=0.1760
Small-tree and shrub spp.	0.13 ± 0.02 a	0.26 ± 0.02 b	0.73 ± 0.32	MPF vs. GPF: F=22.21,p=0.0006 All: F=4.03, p=0.0398
Seed-mass group:				
1 (x ≥ 1.0 g)	0.07 ± 0.02	0.20 ± 0.09	0.19 ± 0.04	MPF vs. GPF: F=2.37, p=0.1520 All: F=1.74, p=0.2091
2 (0.1 g ≤ x < 1.0 g)	0.10 ± 0.01 a	0.21 ± 0.02 b	0.24 ± 0.03 b	MPF vs. GPF: F=19.54,p=0.0010 All: F=13.18, p=0.0005
3 (0.001 g ≤ x < 0.1 g)	-0.01 ± 0.05 a	0.09 ± 0.04 ab	0.54 ± 0.27 b	MPF vs. GPF: F=2.60, p=0.1350 All: F=5.75, p=0.0150
4 (x < 0.001 g)	0.19 ± 0.24	0.71 ± 0.25	1.02 ± 0.62	MPF vs. GPF: F=2.13, p=0.1830 All: F=1.13, p=0.3550
Species:				
Parinari	0.06 ± 0.03	0.22 ± 0.09	0.17 ± 0.04	MPF vs. GPF: F=3.15, p=0.1035 All: F=1.76, p=0.2134
Aglaia	0.13 ± 0.01	0.29 ± 0.06	0.28 ± 0.06	MPF vs. GPF: F=7.86, p=0.0171 All: F=4.45, p=0.0305
Clinostigma	0.12 ± 0.17	0.51 ± 0.30	0.10 ± 0.08	MPF vs. GPF: F=1.11, p=0.3203 All: F=0.75, p=0.4990
Campnosperma	.	.	0.44 ± 0.21	

A discriminant analysis of proportional growth for the four seed-mass groups separated the plot types (Figure 7.16). The first canonical variate explained approximately 93 % of the plot-type separation patterns and produced significant differences among the means (approx. F=3.28, p=0.0113). Proportional growth in seed group 2, which includes species such as *Clinostigma*, *Aglaia*, *Syzygium*, *Garcinia*, *Palaquium*, and *Discocalyx ponapensis* Mez, dominated the first canonical variate: pooled within-class standardised canonical coefficients for CAN1 were 0.3207 (SD1), 0.8808 (SD2), 0.2898 (SD3), and 0.3611 (SD4). Note that overall GPF was more closely associated with SAF than with MPF (Mahalanobis squared distances: MPF-GPF=6.404, MPF-SAF= 12.486, GPF-SAF=2.184).

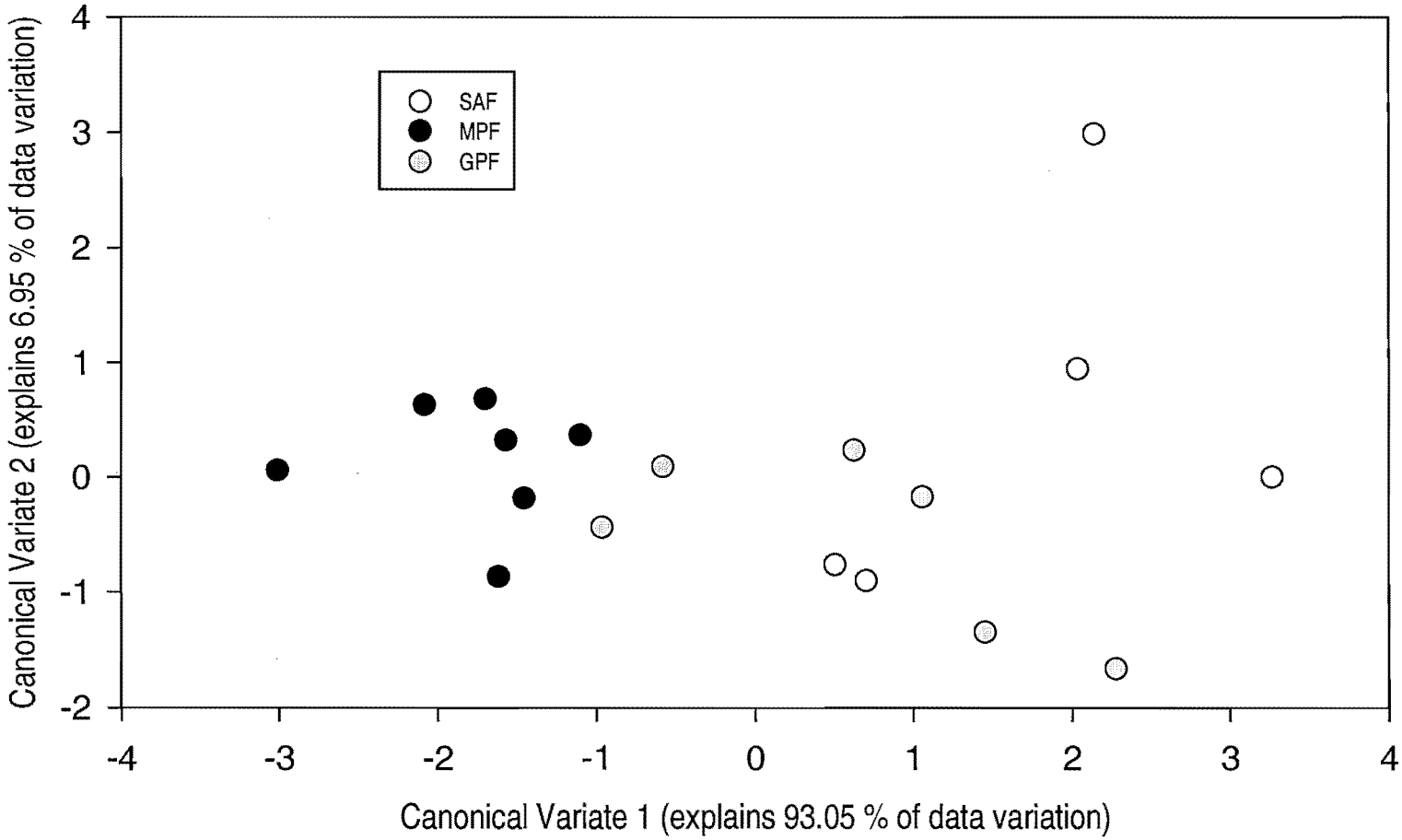

Figure 7.16 Discriminant Canonical Analysis: Mean proportional height growth 0-15 months for seedlings per plot, by seed-mass group.

Proportional (and absolute) height growth among plot types was also analysed, firstly, after removing all individuals recording negative height growth over 15 months (Appendix G), and secondly, including only the one individual per quadrat that recorded the greatest height growth per species or species-group (Appendix H). Mean proportional height growth tended to be considerably greater using positive and maximum height growth than for when negative growth was included, but fewer significant differences were found among the plot types.

Seedling height growth 0-15 months vs. light

Note: in relation to light, results were very similar for absolute and proportional height growth.

Among MPF and GPF quadrats, no significant correlations or linear relationships were found between proportional or absolute height growth and light (DSFC, ISFC, canopy openness) for any species or seed group. Plot mean height growth was significantly positively related to canopy openness for all species combined when MPF and GPF quadrats were analysed together (proportional growth: $F=15.47$, $p=0.0023$, $R^2=58.44$ %, $n=13$), and for seed group 2 ($F=7.40$, $p=0.0199$, $R^2=40.22$ %, $n=13$). Seed group 1 showed weak evidence of a relationship ($F=6.07$, $p=0.0315$, $R^2=35.54$ %, $n=13$) as did its dominant species, *Parinari* ($F=5.37$, $p=0.0407$, $R^2=32.81$ %, $n=13$). Adding SAF to MPF and GPF improves the strength of plot- and quadrat-mean correlations and linear relationships, but results are still variable (Table 7.22).

Among quadrats, absolute and proportional seedling height growth over 15 months tended to increase with decreasing dried-seed mass of a species and was significantly greatest for seed-group 4 (Table 7.23). This trend held, although differences were less significant, even after accounting for an interaction in growth between light and seed-mass groups (Table 7.23).

Table 7.22 Mean (absolute) height growth 0-15 months vs. light.

	Spearman's rank correlations, quadrats			Linear regression, plot means
	DSFC	ISFC	% canopy openness	% canopy openness
All species	R=0.5015, p=0.0001, n=93	R=0.4794, p=0.0001, n=93	R=0.3818, n=301	F=32.27, p=0.0001, R2=66.85 %, n=18
Seed-group 1	R=0.4406, n=56	R=0.4375, n=69	R=0.1773, n=211	F=27.96, p=0.0001, R2=63.61 %, n=18
Seed-group 2	R=0.2869, n=56	R=0.1735, n=56	R=0.3677, n=212	F=12.84, p=0.0025, R2=44.53 %, n=18
Seed-group 3	R=0.0033, n=21	R=0.0195, n=21	R=0.4278, n=68	F=10.19, p=0.0061, R2=40.44 %, n=17
Seed-group 4	R=0.5206, p=0.0387, n=16	R=0.5559, p=0.0254, n=16	R=0.4392, n=62	F=5.09, p=0.0419, R2=28.15 %, n=15
Parinari	R=0.4313, n=63	R=0.4250, n=63	R=0.1491, n=185	F=21.77, p=0.0004, R2=62.61 %, n=15
Cyathea	R=0.6849, p=0.0289, n=10	R=0.7939, p=0.0061, n=10	R=0.5891, p=0.0002, n=36	F=4.32, p=0.0618, R2=28.20 %, n=13

Table 7.23 Quadrat-mean height growth by seed-mass group (all quadrats included) with and without accounting for light levels.
Note: Means for the seed-group effect alone were simple arithmetic means; least-squares means were used to compare seed groups after accounting for significant light x seed-group interactions. Means with different letters are significantly different in an LSD test with α=0.01(arithmetic means) or ls means t-tests with p<0.01.

	Absolute height growth (m)		Proportional height growth	
Seed-mass group	Seed-group effect alone	Light x seed-group interaction	Seed-group effect alone	Light x seed-group interaction
1 (x ≥ 1.0 g),	0.01 a ± 0.01(n=211 quadrats)	0.03 ± 0.01 a	0.11 ± 0.03 a	0.14 ± 0.07
2 (0.1 g ≤ x < 1.0 g),	0.03 a ± 0.01 (n=212)	0.04 ± 0.01 a	0.19 ± 0.03 a	0.20 ± 0.07
3 (0.001 g ≤ x < 0.1 g)	0.06 a ± 0.02 (n=68)	0.04 ± 0.02 ab	0.32 ± 0.09 a	0.27 ± 0.12
4 (x < 0.001 g)	0.23 b ± 0.06 (n=62)	0.12 ± 0.03 b	0.99 ± 0.35 b	0.46 ± 0.14
Test statistics:	Seed-gp. F=3.87, p=0.0094, light (canopy openness) F=89.62, p=0.0001; light x seed-gp F=13.68, p=0.0001		Seed-gp F=5.30, p=0.0013; light F=42.29, p=0.0001; light x seed-gp. F=14.14, p=0.0001	

Relationships between canopy openness and quadrat absolute height growth 0-15 months improved for seed groups 2 to 4 but not group 1 when growth was analysed without negative growth data using Spearman's correlations (c.f. Table 7.22):

Seed-group 1: R=0.1108, n=187;

Seed-group 2: R=0.4835, p=0.0001, n=189;

Seed-group 3: R=0.5493, p=0.0001, n=53;

Seed-group 4: R=0.5261, p=0.0002, n=45.

Height growth among cohorts

Table 7.24 Proportional height growth 3-15 months among recruitment cohorts, for seedlings in MPF and GPF pooled.
Means with different letters are significantly different in an LSD test with α=0.01.

	Individuals existing at time0	Newly recruited at 1 month	Newly recruited at 3 months	ANOVA, cohort effect:
All spp. combined	0.04 ± 0.02 a	0.29 ± 0.11 ab	0.74 ± 0.26 b	F=5.26, p=0.0110
Life-form:				
Large (and medium)-tree spp.	0.01 ± 0.02 a	0.41 ± 0.18 ab	0.85± 0.36 b	F=3.86, p=0.0325
Small-tree and shrub spp.	0.14 ± 0.03	0.07 ± 0.07	0.34 ± 0.14	F=1.67, p=0.2125
Seed-mass group:				
1 (x ≥ 1.0 g)	0.00 ± 0.01 a	0.41 ± 0.18 ab	0.99 ± 0.47 b	F=3.69, p=0.0388
2 (0.1 g ≤ x < 1.0 g)	0.08 ± 0.02 a	0.09 ± 0.07 a	0.54 ± 0.23 b	F=1.64, p=0.2169
3 (0.001 g ≤ x<0.1g)	0.03± 0.04 a	0.05 ± 0.19 a	0.44 ± 0.20 b	F=16.75, p=0.0001
4 (x < 0.001 g)	0.38 ± 0.15	.	.	.
Species:				
Parinari	0.01 ± 0.01 a	0.41 ± 0.18 ab	1.14 ± 0.51 b	F=4.26, p=0.0255
Aglaia	0.12 ± 0.04 a	0.08 ± 0.07 a	0.41 ± 0.19 b	F=0.59, p=0.5661
Clinostigma	0.16 ± 0.12	0.18 ± .	1.71 ± .	F=6.45, p=0.0215
Campnosperma	.	.	0.66 ± 0.22	.

Seedling proportional height growth over 3-15 months tended to be greater for new recruits than for plants already present at time 0 (Table 7.24). In particular, proportional height growth of the three-month recruits was often significantly greater than the time 0 plants. However, variation was high within each cohort and sample-sizes for some cohorts and species/groups were small. Results were pooled among plot types because with the exception of seed-group 3 between MPF and GPF (plot type x

cohort, F=20.01, p=0.0001), there were no significant plot type x cohort interactions in any analysis and few significant plot type differences for individual cohorts within species groups (see Appendix I). Note also that although most results were very similar with and without SAF, Table 7.24 results excluded SAF. As SAF growth overall was greater than the forest plots but new recruits were not censused at one month, in several cases with all three plot types pooled, one-month recruits grew less than the time 0 cohort because the time 0 (and three-month) growth included fast-growing SAF plants.

Size vs. growth among cohorts

Initial seedling and sapling height did not relate to growth for any seed-mass group or species from the time 0 cohort, but sapling data were limited. Among new recruits, height growth decreased significantly with increasing initial size for *Parinari* seedlings (Figure 7.17; initial height transformed by the negative exponential function, model: F=6.80, p=0.0144, n=30 quadrats). However, high data variability limited the predictive power of the relationship (R^2 =19.55 %). Initial size affected no new recruits from other seed-mass groups or species significantly, although this was due, in part, to having few data for one-month and three-month new recruits. Recall that new recruitment was low during the drought, and the abundant 15-month recruits were measured only once.

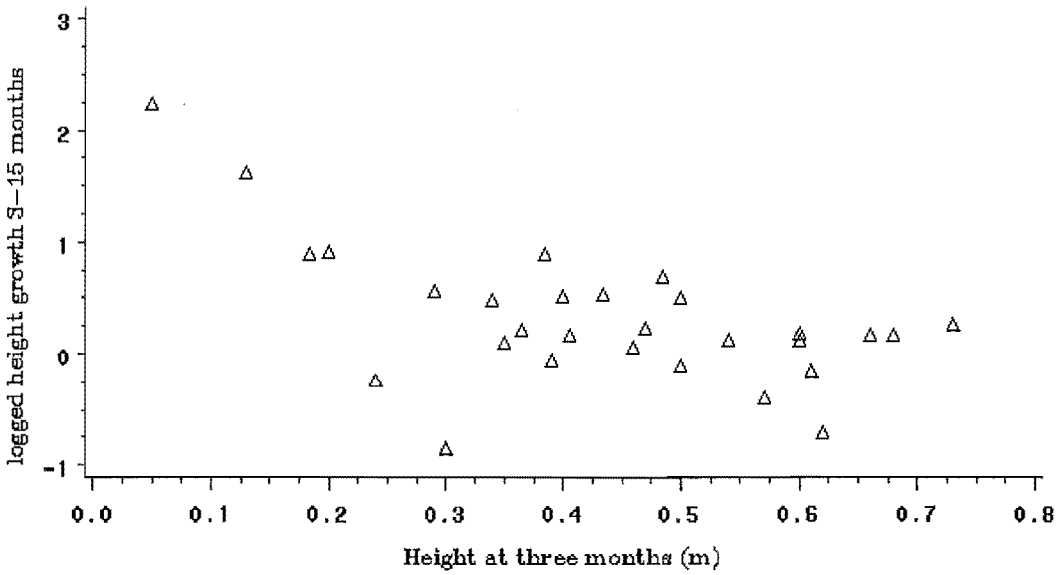

Figure 7.17 *Parinari* new recruitment, height at three months vs. height growth 3-15 months.

7.2.4 Mean diameter growth

With all species and heights combined[15], diameter growth and proportional diameter growth over the 15 months were very small, but they were significantly greater in SAF than in MPF or GPF (Table 7.25).

Table 7.25. Mean dbh growth for all surviving individuals
Means with different letters are significantly different in an LSD test with α=0.01.

	MPF	GPF	SAF	ANOVA statistics
Mean diameter growth (cm)	0.20 ± 0.03 a	0.23 ± 0.05 a	0.68 ± 0.21 b	MPF vs. GPF: F=0.37, p=0.5533 All: F=6.01, p=0.0121
Mean proportional diameter growth (cm)	0.03 ± 0.01 a	0.04 ± 0.01 a	0.26 ± 0.08 b	MPF vs. GPF: F=0.80, p=0.3889 All: F=12.45, p=0.0007

7.3 Non-woody Species

Recall that there were no significant differences in non-woody coverage between MPF and GPF at time 0 (Table 6.2). Over the next 15 months, mean non-woody coverage (per square metre) changed in both MPF and GPF (time: F=8.52, p=0.0069), but both forest plot types followed the same pattern (plot type x time: F=1.03, p=0.3912). That is, both plot types' non-woody cover decreased significantly during the drought months (time 0-3 months: F=10.79, p=0.0073), and increased again after the drought (time 3-15 months: F=8.10, p=0.0159) (Table 7.26).

Sub-grouped by life-forms, individual life-forms responded differently through the study period (time x life-form: F=3.02, p=0.0098), mostly during the first three months (time 0-3 months: life-form: F=5.16, p=0.0036), but there were no interaction effects between the two plot types. GPF cover did bounce back more than MPF after the drought, most notably in lianas, but plot type changes were still not significant in that year (3-15 months, plot type effect: F=2.27, p=0.1602).

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[15] Diameter growth was not sub-grouped by size-class, seed-group or life-form because there was insufficient data for seed groups 3 and 4 to avoid missing values, and shrubs and small-tree species were rarely large enough to have had diameters at 1.3 m ≥ 1 cm.

Table 7.26 Mean percentage area-cover per m^2 by non-woody life-forms over 15 months.

Plot type	Life-form	Mean % area-coverage / m^2 ± s.e. (% quadrats represented, in brackets)		
		TIME 0	3 months	15 months
MPF	All species combined:	2.31 ± 0.82 (58 %)	1.69 ± 0.52 (54 %)	1.95 ± 0.59 (64 %)
	Ferns	1.42 ± 0.56 (28 %)	0.88 ± 0.29 (23 %)	0.98 ± 0.40 (25%)
	Grasses	0.0 (1 %)	0.00 (1 %)	0.02 ± 0.02 (1 %)
	Herbs	0.10 ± 0.07 (4 %)	0.14 ± 0.11 (4 %)	0.18 ± 0.15 (4%)
	Lianas	0.79 ± 0.40 (48 %)	0.67 ± 0.33 (46 %)	0.77 ± 0.31 (54 %)
GPF	All species combined:	2.23 ± 0.65 (65 %)	1.74 ± 0.53 (59 %)	2.39 ± 0.56 (75 %)
	Ferns	0.82 ± 0.35 (25 %)	0.71 ± 0.30 (24 %)	0.92 ± 0.34 (21 %)
	Grasses	0.00 (0 %)	0.00 (0 %)	0.00 (1 %)
	Herbs	0.47 ± 0.33 (5 %)	0.40 ± 0.26 (4 %)	0.51 ± 0.31 (7 %)
	Lianas	0.94 ± 0.19 (57 %)	0.63 ± 0.14 (50 %)	0.95 ± 0.15 (72 %)
SAF	All species combined:	31.54 ± 4.65 (100 %)	32.39 ± 4.17 (100 %)	34.88 ± 4.03 (100 %)
	Ferns	20.21 ± 3.26 (97 %)	20.31 ± 3.44 (99 %)	26.73 ± 5.01 (96 %)
	Grasses	6.75 ± 3.03 (54 %)	7.55 ± 3.18 (57 %)	3.31 ± 1.94 (54 %)
	Herbs	1.50 ± 0.33 (25 %)	1.70 ± 0.43 (28 %)	1.84 ± 0.65 (31 %)
	Lianas	3.09 ± 0.80 (74 %)	2.83 ± 0.47 (76 %)	3.01 ± 0.71 (77 %)

Compared with the two forest plot types, mean area-cover by non-woody species in SAF was vastly different at time 0 and these initial differences remained over the 15 months (Table 7.26; all plot types x time: $F=1.69$, $p=0.1798$). The most observable changes in SAF were the considerably reduced grass cover and increased fern cover over 3-15 months as trees and taller ferns shaded out the grasses. In contrast to MPF and GPF, coverage of non-woody species in SAF was not reduced during the drought.

7.4 Summary

- Changes in light pre- vs. post-gap were highly variable. On average, canopy openness increased after gaps were created but in many quadrats it actually decreased. After gaps were opened, canopy openness in GPF was significantly greater than in MPF when compared alone, but they were still both vastly darker than the very open SAF. Light-sensitive photo-papers recorded significantly higher light levels at 3 m above the ground than at 1 m, especially in SAF.
- Leaf-litter coverage changed very little in the first three months of the study. (It was not measured beyond three months.) Litter depth in MPF and GPF increased during the drought then remained similar. SAF litter depth did not change appreciably during the drought but increased over the following year so that by 15 months, SAF litter depth was no longer significantly less than MPF or GPF. Woody debris cover in GPF increased dramatically after gaps were opened.
- Stem frequencies in MPF and GPF decreased during the drought months, then increased in the year after. The influence of the drought was strongest among seedlings and for certain individual species, namely *Campnosperma* and *Clinostigma*. For example, by the one-month re-census, approximately one quarter of all seedlings in MPF and GPF had died, and for *Clinostigma* and *Campnosperma* seedlings, mortality was more than 50 %. With its large seedlings and seed-mass, *Parinari* were better able to withstand dry conditions. In contrast to the forest plot types, SAF stem frequencies did not fluctuate much during or after the drought. Overall, mortality tended to be greater in GPF than in MPF at any time, and SAF relative mortality per month was less than for the forest plots during the drought period but greater during the wet period.
- Among the initial time-0 seedling population, the taller the individual the greater was its chance of survival. Over the 3-15 month period, seedling survival for a particular recruitment cohort tended to be greatest in MPF and least in SAF, but in all plot types, older individuals had a greater chance of surviving than did newer recruits.
- The dominant contrasts apparent between MPF_{pooled} and SAF at time 0, with respect to seed-group frequencies - the heaviest two seed-groups were associated with the forest plots and the lightest two with SAF - were similar for individuals newly recruited over 15 months. In MPF and GPF quadrats, *Clinostigma* and *Campnosperma*

recruitment was positively correlated with light. In contrast, *Parinari* recruitment was strong and negatively correlated with light.

- By 3 months, there was still a higher proportion of healthy seedlings and saplings in SAF than in MPF and GPF. GPF contained a significantly lower proportion of healthy seedlings than MPF, due mainly to more physical damage in GPF following gap openings.

- Overall, SAF had significantly greater proportional height growth for both seedlings (≤ 1 m height) and saplings (1-4 m height) over 15 months, but there were no significant differences between MPF and GPF. Among individual sub-groups, growth tended to be higher in GPF than in MPF, and was significantly greater in GPF than in MPF for small-tree and shrub species, and seed-mass group 2 species (includes species such as *Aglaia*, *Clinostigma*, *Syzygium*, and *Palaquium*). High plant variation and sometimes low plot-mean sample sizes meant that growth in SAF was only significantly greater than MPF for seed-groups 2 and 3, and was never significantly greater than GPF. Height growth tended to be positively correlated with light for each seed-mass group but results varied depending upon the size-class analysed (seedlings vs. saplings), whether plot or quadrat-level data were analysed, and whether MPF and GPF were analysed alone or with SAF. Among recruitment cohorts, seedling growth 3-15 months tended to be greater for new recruits than for those plants already present at time 0, particularly those newly recruited at three months.

- Diameter growth was very small over 15 months but overall growth in SAF was significantly greater than in either of the two forest plot types.

- Non-woody cover was vastly greater in SAF than in MPF and GPF at all times. SAF cover barely changed during the drought, but non-woody cover in the two forest plot types suffered during the drought. In the following year, cover in MPF and GPF mostly regained what had decreased during the drought, but in SAF, grass cover decreased and fern cover increased markedly.

- Correlations among light measures and between light measures and various plant response variables showed that the site factors derived from hemispherical photographs most closely reflected environmental conditions for plants. Photo-papers and canopy openness from the spherical densiometer were less powerful at the quadrat level of analysis, but were effective at the plot level. Correlation strengths for all light measures deteriorated markedly in low light.

Discussion and Conclusions

Chapter Eight: Forest Dynamics in Pohnpei's Uplands

The aim of this research was firstly, to examine the role of advance growth in gap-phase regeneration in Pohnpei's upland rainforest. This was pursued by tracking advance growth from mature-phase forest through to the gap phase. The second aim was to compare this picture of advance growth and natural forest regeneration with regeneration in cleared upland-forest areas after cessation of sakau (*Piper methysticum*) cultivation. Finally, I sought to understand the implications of these differences for forest restoration strategies.

8.1 Natural disturbance regime for upland forest

The preliminary disturbance survey found a range of disturbance scales operating within the forest, with small-scale and very localised disturbance by *Clinostigma* fronds (although fronds were not recorded), branches, and sub-canopy small trees being most common. Less-frequent but larger-scale disturbances were caused by individual tree deaths, either standing dead, uprooting, or snapping. Overall, the larger the gap-initiator the more rarely it occurred, as has been recorded in other forests (Yavitt et al. 1995; Arevalo & Fernandez-Palacios 1998; Arriaga 2000). It was at the disturbance scale of single-tree falls that GPF was created from MPF. Small gaps such as these and branch-falls dominate the forest-patch-level regeneration in many tropical rainforests (Hartshorn 1978; Lang & Knight 1983; Uhl et al. 1988; Brokaw 1996; Green 1996). Small single-tree-fall gaps on Pohnpei also represented the most common disturbance that was practical to study.

The disturbance survey, though limited in its scope, recorded 46 adult canopy trees dead in two hectares, 28 % of which were standing dead, 48 % were uprooted, and 24 % were snapped. Among sub-canopy tree-fern deaths (131), 36 % were standing dead and 58 % uprooted. Disturbance frequencies found in this study are difficult to compare with other forests because the sample was small and because species-specific decomposition rates, which are unknown for Pohnpei, may have

confounded disturbance rates. For example, I observed that *Clinostigma* decomposes rapidly once it dies whereas *Cyathea* trunks disintegrate very slowly. It is clear though that for both sub-canopy and canopy disturbances on Pohnpei, trees were uprooted more commonly than dying standing.

Although I did not attempt to measure gap area, Uhl et al. (1988) found that tree-fall gap size correlated roughly with the size of the fallen tree. They found that trees 20-50 cm dbh generally formed small gaps (5-100 m^2) when they died, while gaps created by trees 50-100 cm dbh were usually 100-200 m^2. The initiators of my experimental gaps had dbh measures of 30-55 cm, so they would be classed as small gaps. Furthermore, Pohnpei's relatively low canopy height (see Chapter 3.5) likely creates smaller single-tree-fall gaps than would taller trees with similar diameters.

Factors affecting the small-scale gap disturbance regime and gap size include rainfall, topography and soils (Kapos et al. 1990), and tree species, particularly their wood properties (Putz 1983; Arriaga 1988) and crown width (Canham et al. 1990). Pohnpei's forests generally grow on steep, fairly deep but often rocky soils; rooting depth of trees is often shallow (personal observation). These characteristics may explain the predominance of uprooting found in the disturbance survey although Pohnpei's relatively low canopy height may afford trees greater stability (Kapos et al. 1990) and reduce the gap area created when they do fall.

Tropical cyclones and hurricanes are a major cause of multiple tree-falls in forests located within approximately 10-20 degrees latitude (Whitmore 1974; Frangi & Lugo 1991; Walker 1991; Yih et al. 1991; Bellingham et al. 1992; Arriaga 2000). Pohnpei (6 degrees latitude) lies just outside this main typhoon, and multiple-tree falls were rare in the upland forest. Still, the island does receive moderate tropical cyclones (called typhoons in the Western Pacific) that affect localised forest areas on average about once per decade (W. Raynor, pers. comm. 2000), and a rare strong typhoon can devastate large areas. The eye of a large typhoon crossed over Pohnpei in April 1905, severely damaging the island, including almost all buildings and most agro-forest trees (toppled or defoliated) (Berg 1905), and apparently much of the upland forests (W. Raynor, pers. comm. 2000). The return time of this scale of typhoon is unknown; it could be once per century or once per few to several hundred years. If the return time is once every few hundred years, then the canopy trees may be in a relatively young stage after 1905 and will eventually grow larger, thereby increasing the size of the single gap-initiator. If the return time of the large-scale

disturbance is relatively short, however, say once every one hundred years, then canopy trees and hence patch gaps will rarely, if ever, be larger than they are now.

Thus, the natural-forest disturbance regime on Pohnpei operates at multiple and overlapping temporal and spatial scales. The Pohnpeian flora is adapted to this natural disturbance regime as described in my disturbance survey. In particular, a large advance-growth population is common in forests exposed to mostly small-scale disturbances, which promote understorey seedling and sapling reinitiation (Oliver & Larson 1996, p.129). Conversely, *Campnosperma*'s presence in mature-forest canopies and its abundant but poorly surviving seedling recruitment indicates the long-term occurrence of much larger disturbances. The characteristics of *Campnosperma* plus the presence of a number of native and endemic early-successional species such as *Macaranga carolinensis* var. *grandiflora* Pax & Hoffman illustrate that large disturbances (from typhoons) are an integral part of the long-term forest dynamics on Pohnpei. In the Solomon Islands, *Campnosperma* regeneration usually follows cyclones (or logging) (Whitmore 1974).

The common hardwood canopy species *Campnosperma*, *Myristica*, and *Parinari* were chosen as the gap-initiators in my artificially created gap-phase forest plots (rationale outlined in Chapter Six). For practical reasons, trees were felled rather than uprooted. Not all tree species on Pohnpei naturally create a gap the size of the hardwood adults since species vary in their stature, wood density, and canopy architecture, and therefore create different kinds of gaps. *Clinostigma* was the most common gap initiator among adults but it was not chosen for GPF gaps because its crown was so small that experimentation would be difficult. *Clinostigma* usually uprooted whereas *Parinari* most commonly died standing. Nevertheless, large adults of *Campnosperma*, *Myristica*, and *Parinari* often were found snapped rather than uprooted so the artificial gaps mimic this type and scale of disturbance. Although it was not examined, the type of gaps created in GPF plots may be less appropriate on some slopes than others due to differences in forest structure. Gaps may also be more naturally frequent on steep forest slopes than on more gentle slopes (Clark et al. 1996). However, detailed topographic controls were beyond the practical capabilities of this research because of the difficulty in finding sizeable areas of intact forest within the mid-uplands.

In contrast to the natural disturbance regime in the upland forests, sakau plots in Pohnpei's uplands range from approximately 400 m^2 to over 4000 m^2 in area (Allum 1996). The SAF plots are therefore more similar in size to rare natural, large, multiple-tree-fall gaps caused by events such as wind-storms (e.g., Uhl et al. 1988). Very severe wind events that affect some tropical areas can create gaps covering many hectares (reviewed in Whitmore & Burslem 1998). The moderate typhoons and the much rarer 1905-level typhoon on Pohnpei likely create gaps within or even extending beyond the size of SAF plots. However, although the upland forest can be disturbed on the same size scale naturally as the majority of sakau plots, the process of cultivation creates marked differences in regeneration patterns between natural and human-induced disturbance conditions. Allum (1996) found that both the length of time that plots are cultivated and the size of plots affect species assemblage patterns. Large, long-cultivated plots had species assemblages in greatest contrast with intact forest, while small plots cultivated for shorter periods before abandonment were most similar. My SAF sites were cultivated for a relatively short time (3-11 years, c.f. some of Allum's (1996) old sakau plots were cultivated for 20-30 years), and small-medium, that is, 1000-2000 m^2 in area (Table 4.2).

8.2 Plot types at time 0

Understorey light levels in most tropical rainforests are 0.5-5 % of PAR received in the open (Chazdon & Fetcher 1984a; Canham et al. 1990; Smith et al. 1992; Rich et al. 1993; Whitmore et al. 1993; Clark et al. 1996). In a large light survey at La Selva, Costa Rica, for example, only 3 % of (615) global-site-factor (GSF) measurements at one metre above the ground were greater than 5 % and only 1 % of measurements were more than 10 % of PAR received in the open (Clark et al. 1996)[16]. The proportions of direct and diffuse light comprising GSF (DSFC and ISFC, respectively) are unknown for my forest sites on Pohnpei. Nevertheless, I can calculate GSF using a range of possible ratios between direct and indirect site factors from hemispherical photographs that cover results from other tropical forests (0.3 up to 0.7 for each factor). GSF in mature-phase plots then was 3-5 % of PAR, which is

[16] A global site factor (GSF) measures the total site-specific amount of direct and indirect PAR at a (forest) site compared with in the open.

at the more open end of the light range quoted above for other tropical rainforests. In contrast, GSF for sakau-agro-forest was 24-27 % of PAR in the open. Similar to GSF results, mean canopy openness as measured with a spherical densiometer was 5 % for MPF versus 25 % for SAF. Moreover, the maximum canopy openness in a quadrat in MPF was 13 % whilst in SAF it was 97 % (minima were 1.8 % and 2.1 %, respectively). Sakau-agro forest (SAF) plots were thus considerably larger (see previous page) and therefore more open and brighter than the forest. SAF plots were also vastly more spatially variable in light conditions within plots than MPF because they ranged from central, very open areas out to edges with more intact forest as well as some remnant adult trees within plots.

Leaf litter covered a smaller area in quadrats and was shallower in SAF than in MPF at time 0. The area covered by rocks and large buttress roots was highly spatially variable within plot types but tended to be much less in SAF than in MPF. This was because fewer large, buttressed trees remained in SAF than in MPF, and sakau cultivators generally chose the least rocky forest sites for growing sakau.

Plant species results were similar to Allum (1996). Her study and this one found no significant differences between MPF and SAF in species richness, even though more species were recorded in SAF than in MPF because of its greater range in micro-environmental conditions. Ten species in my study (five trees and five vines) were common to each plot type's 20 most widely present species. Yet, only one of the top five species in terms of presence/absence (*Piper ponapense*) and four of the top ten (*Piper*, *Campnosperma*, *Aglaia*, *Freycinetia ponapensis* Martelli) were common to both plot types. *Piper* and *Campnosperma* were also common species in the seed rain and soil seed banks of both MPF and SAF (Gardner 1997; Winthrop 1998). I found that species presence in quadrats was aligned along a light gradient, and to a lesser extent, a litter-volume gradient, which itself was related to light. However, this gradient reflects a much wider light range than is found in small-scale forest dynamics, that is, in the absence of a typhoon; species presence in MPF and GPF quadrats at time 0 (and 15 months) did not discernibly relate to light when I excluded SAF from the analysis.

Among woody species and with all plot types combined, seedling frequencies of the heaviest two seed-mass groups were negatively correlated with quadrat light levels at time 0, seed-group-3 frequencies were uncorrelated, and seed-group 4 was positively correlated with quadrat light. With the exception of *Campnosperma*, whose

seedlings can germinate under closed forest but seldom survive more than a few weeks, very few early successionals were present, even briefly, in MPF at time 0. This is not surprising since early-successional species usually make up only a small proportion of species and individual plants in closed-canopy, mature-phase forests elsewhere; most are late successionals (Whitmore 1984). These results illustrate the dichotomy of early-successional tree species, which mostly occur in large gaps, versus late-successional species, which generally occur in lower light areas such as closed-canopy forest (Hartshorn 1978; Denslow 1980; Whitmore 1984; Brokaw 1985b). However, in line with Barton (1984) and Devoe (1990; 1992), quadrat ordinations indicate that species are partitioning the light gradient within and among plots rather than behaving as if particular-sized gaps were homogeneous.

On Pohnpei, Winthrop (1998) found that heavy seeds fell frequently in the MPF seed rain and rarely in SAF; conversely, light seeds fell frequently in SAF but were rare in MPF. Only *Piper* and *Clinostigma* dispersed more than 20 seeds into both plot types. The most widely present woody species in the seed rain in MPF were *Campnosperma*, *Clinostigma*, and to a lesser extent, *Ficus*, while the most numerous were *Fagraea berteria* var. *sair* (Gilg & Benedict) Fosberg, *Campnosperma*, *Clinostigma*, and an unknown species. With the exception of *Clinostigma*, the other most numerous seed-rain species were not abundant in my MPF. Although *Campnosperma* seedlings commonly recruit into MPF, the seedlings never survive more than a few weeks in the forest shade and consequently do not become saplings or larger individuals in MPF.

Gardner (1997) also found heavier seeds were more common in the Pohnpeian soil seed bank of MPF than in SAF. *Clinostigma* and *Campnosperma* were the most common tree species present in the MPF seed bank (Gardner 1997) and both species were amongst the five most common tree species in the standing tree population of MPF. Yet, *Campnosperma* does not successfully regenerate in MPF. Furthermore, Gardner (1997) suspected that *Clinostigma*'s presence in the seed bank was an artefact of recent copious seed production rather than persistence in the seed bank. *Macaranga* was also a common seed bank species, but consistent with its early-successional status and presence in the seed bank, I never recorded it in my MPF plots. Hence, similar to Williams-Linera's (1993) findings in Mexico, the MPF seed bank does not reflect the present mature-forest composition and structure.

In contrast to MPF, the seed bank better represented the standing vegetation in SAF, although it was not the sole contributor of propagules. Grasses were the most frequently occurring seed-bank species in SAF, along with *Piper*, *Morinda*, *Cyrtococcum patens*, and other small-seeded species (Gardner 1997). In the standing vegetation, grasses, *Piper* and *Morinda* were all common in SAF, but I never recorded *Cyrtococcum patens*, and neither did Allum (1996).

Uhl et al. (1988) found that gap-phase forest plots where advance growth was removed had less than half the woody plant density of the non-cleared plots, even after four years. Results from the present research agree with that study: SAF plots largely clean-weeded of advance growth had less than half the number of trees and shrubs than MPF. In spite of this, six of the ten most abundant species were the same in the two plot types, and three of the top five were in common (*Campnosperma*, *Aglaia*, and *Parinari*). Nevertheless, distributions of absolute stem frequencies and size-class, plus ranks in species presence among quadrats illustrated that the overall dominance of these common tree species was very different in MPF and SAF. In particular, non-woody species dominated the presence/absence ranks, and most woody species were present in SAF more as saplings without the large advance-growth seedling populations for the late-successional species that were so abundant in MPF.

Patterns of physical damage among seedlings and saplings differed slightly between MPF and SAF at time 0. Many seedlings were bent in MPF because of fallen *Clinostigma* fronds; *Parinari* was bent most often. In contrast, both *Clinostigma* fronds and *Parinari* seedlings were lacking in SAF so time-0 health results showed a lower proportion of bent seedlings. Conversely, a slightly greater proportion of saplings was bent in SAF than in MPF. This was probably due to woody debris that fell when the sakau plots were initially cut (the area covered by woody debris was greater in SAF than in MPF at time 0) as well as rapid but unstable growth of some species.

The group of mature-phase plots that became gap-phase after trees were felled at time 0 (GPF) was largely similar to mature-phase MPF plots at the initial census (Chapter 6.2.1). No significant differences existed between MPF and GPF at time 0 for the micro-environmental variables or for any biotic variables that compared totals or means with all species combined. Separated by life-form, seed-mass group, or

individual species, however, tree and shrub stem frequencies showed more spatial variability. For example, distributions of the dominant canopy species were patchy: significantly more *Clinostigma* occurred in GPF than in MPF plots at time 0, while the opposite was true for *Parinari* and *Myristica*. The patchy occurrence of these three species strongly contributed to significant time 0 differences in stem frequencies between the plot types for seed groups 1 and 2. High within-plot-type and within-plot variability illustrates that the notion of mature-phase forest plots being homogeneous controls is not strictly true.

Factors that could have influenced spatial variation of species within the mature-phase forest plots include topography and soil type, aspect, elevation, and disturbance history. All forest plots were sited between 260 m and 420 m elevation, which is within the elevation range for upland broadleaf forest and below the elevation where *Clinostigma* alone tends to predominate (see Chapter 3.5, and MacLean et al. 1986). The forest plots were sited facing an easterly (windward) direction rather than a westerly (leeward) direction in an attempt to control for any major differences in rainfall. The small area of forest practically available for study, however, precluded controlling for topography; plots ranged from flat or gently sloping, through to very steep. The relationships between landforms, soils, and vegetation patterns within upland broadleaf forest are unknown. Such a study would be very insightful, but it would be difficult to find sufficiently large contiguous areas of intact forest.

Dispersers also play a role in creating patchy forest composition patterns on Pohnpei. Juveniles of large-seeded species, especially of *Parinari* and *Myristica*, tend to germinate under conspecific adults. *Parinari*'s fruits are very large and heavy (spheres ~5-8 cm diameter, average dried-seed-mass is 40.86 g) and lack any disperser on Pohnpei other than gravity. *Myristica* fruits are also large and heavy (3-4 cm width by ~ 5 cm length, average dry-seed mass 12.79 g). In other tropical forests, the bright red or yellow arils on the fruits of species within Myristicaceae attract large birds and/or small mammals (Whitmore 1972; Howe et al. 1985; Cooper 1994). On Pohnpei, stomach analyses of the Micronesian pigeon (*Ducula oceanica*) have found *Myristica* fruits (D. Buden, pers. comm. 2000), but it is likely to be the only bird on Pohnpei with a large enough gape to eat these fruits. Bats may also be important fruit dispersers as they are in other tropical forests, but the foraging habits of the two Pohnpeian bat species is not well known. As it is elsewhere, seed rain in Pohnpei's

mature-phase forest is spatially variable, although seed rain was more evenly distributed in MPF than in SAF (Winthrop 1998).

The Micronesian pigeon population is not rare on Pohnpei, but numbers have been relatively low since the late 1920s due to professional hunting during the Japanese era (Baker 1951). *Clinostigma* fruits are considerably smaller than those of *Parinari* and *Myristica* and therefore are able to be eaten by relatively common, fruit-eating birds such as the Micronesian pigeon, Pohnpei lory (*Trichoglossus rubiginosus*), and the purple-capped fruit dove (*Ptilinopus porphyraceus*). Nevertheless, all these bird species appear to have declined dramatically since at least the mid-1980s (Buden 2000), or earlier for those professionally hunted in the Japanese era. Unrestricted hunting and major habitat losses are most likely the major causes of bird decline (Buden 2000, personal observations). Also, Pohnpei has introduced rats but no native small terrestrial animals. Species clumps could therefore relate partly to a lack of density-dependent seed and seedling predation under conspecific adults as has been shown to affect species distributions in some forests (Augspurger 1984b; Connell et al. 1984; Becker & Wong 1985; Sork 1987; Schupp 1988b).

8.3 Micro-environmental changes among plot types over 15 months

The only treatment difference in GPF compared to MPF after time 0 was the felling of a tree in each plot (other secondary trees were sometimes felled if within the felling path). When the trees fell in GPF plots, immediate physical changes included elevated light levels and increased woody debris.

8.3.1 Light

The light environment within small Pohnpeian gaps showed a more complex picture of gap-phase forest than is often presented (Chapter 7.1.1), particularly compared to studies that characterise light in gaps only using data from gap centres (e.g., Chazdon & Fetcher 1984a; Lee 1987; Brown & Whitmore 1992). My results do not so much contradict the gap-non-gap dichotomy from such studies: canopy openness at the "gap centre" as estimated by the maximum light measurement per plot was significantly greater in post-gap GPF than in MPF ($F=17.63$, $p=0.0015$, $n=13$

plots). Nevertheless, results from the present study show explicitly the spatial variation and subtleties of change for areas lying within that dichotomy. The main change in the GPF light environment in each plot post-gap-opening was an increase in the heterogeneity of light conditions in the forest, without necessarily increasing significantly the average light condition, particularly in the case of ISFC and DSFC. These results support studies that have found substantial spatial and temporal variation in the light environment within gaps and within mature forest (e.g., Raich 1989; Devoe 1990; Smith et al. 1992; Clark et al. 1996). In addition, photo-paper results, which showed greater differences in the GPF environment and between GPF and MPF at three metres in height than at one metre, indicated that absolute light changes were greater for saplings than for seedlings.

The more complex picture of light in gap-phase forest here arises for several reasons. Firstly, two levels of analyses were used in this study. At a broad scale, I classified forest areas as either gap- or mature-phase in the style of the gap-non gap dichotomy. Plots contained and averaged data from 20 quadrats randomly laid out within a 15 m radius. However, a gap plot encompassed not only the central gap zone but out to where the gap grades into mature forest. I had in mind Raich's (1989) results of light infiltrating up to 20 m from the physical gap edge in a Malaysian forest similar in its height of emergents (30-37 m) to Pohnpeian forest (~35 m, see Chapter 3.5). Consequently, the gaps as I delineated them undoubtedly comprised quadrats that would not be classed as "gap" in other gap-non-gap studies. Some of my GPF plots were right in the gap impact zone and became heavily covered and thus darkened by debris. Other quadrats were near the crown, near the stump, or up to 10-15 m away from the closest part of the fallen tree(s). I could have used, say, a ten-metre radius instead of a fifteen-metre one to concentrate the quadrats and perhaps thereby increase the dichotomy between MPF and GPF plots. Yet, the crown debris area and quadrats close to or downhill from it would have still shown a reduced light effect, and quadrats near the stump and on the unshaded side of the gap would have shown increases in light. In addition, I wanted to use the same plot radius within SAF plots. Preferably, all plots should have faced the same aspect and slope, but I could not find such plots in the small area of forest that was practically available for study. In further contrast to other studies, plot centres were cited to maximise the buffer distance to edges with forest cleared for sakau cultivation, so trees were felled near the edge of the plot and through the centre point rather than the stump of the felled

tree being the plot centre. The GPF plots in this study, therefore, represent the mean response of variables encompassing the direct impact zone of a gap but also grading into mature forest.

To complement and interpret with the plot means, I analysed light vs. plant responses using the one-metre-square quadrats as the units of observation rather than plots. Quadrats represented the abiotic environment independent of the gap-non-gap dichotomy and thus illustrated the continuum of disturbance and light levels in a forest[17]. This approach parallels an increasing number of studies that are expressing more realistically the complexity of the forest light environment and plant responses to it (e.g., Barton 1984; Hubbell & Foster 1986b; Raich 1989; Canham et al. 1990; Denslow et al. 1990; Lawton 1990; Turner 1990b; Devoe 1992; Smith et al. 1992; Clark et al. 1996).

Secondly, species composition and differences in the architecture of the main canopy species can influence the light levels in forest patches (Canham et al. 1990; Kabakoff & Chazdon 1996). This was apparent in the mature-phase forest plots before gaps were created. For example, *Clinostigma* palm has a small frond mass atop a slender, branch-less trunk. *Campnosperma* has a large but open crown, branching only near the top of the tree; leaves are long (up to ~ 60 cm), widely spaced in a spiral, and quite thick. In contrast, *Parinari* and *Myristica* adults have dense crowns with branches and leaves down most of the trunk. When all four species occur together, *Clinostigma* (25-~35 m average adult height) and *Campnosperma* (25-30 m average adult height) emerge above the heavily leafed and branched *Parinari* (15-25 m) and *Myristica* (20-25 m). Where the adults of *Parinari* and *Myristica* were rare or absent, the forest plots were more open because only the spacious *Clinostigma* and/or *Campnosperma* were in the canopy. Consequently, means of light measures in my study, particularly for the hemispherical-photograph sub-sample, were (non-significantly) higher in GPF (it has less *Parinari* and *Myristica*) than in MPF at time 0. Architectural characteristics of the canopy trees, a relatively short forest stature, and perhaps topography in the steep plots due to lateral light patterns, result in a more open mature-forest micro-environment on Pohnpei than at some other sites (GSF was 3-5 % PAR vs. 0.5-5 % elsewhere, see p.159). Subsequently, the post-gap light environment contrasted less with mature forest on Pohnpei than it might in forests that

[17] Note: only seedlings (≤ 1 m height) in the 1 m^2 were included in quadrat-level analyses.

are taller and have mostly densely crowned canopy species. In addition, the relatively short adult trees produced small gaps, so again, pre- vs. post-gap contrasts were smaller.

The height at which light was measured introduces further variation in the light environment and represents reality for some plants more than others. Most light readings were at one metre in height. Among seedlings, this height was appropriate for *Parinari* advance growth that sit at 60-100 cm in height, but the light environment for much smaller advance growth such as *Clinostigma* and *Aglaia* (10-20 cm height) could be considerably darker and more variable. This may partially explain why *Parinari* seedling relationships with light were usually stronger than other species, together with their larger sample size. Had I also measured light with photo papers at ground level, these light patterns may have been better elucidated. Unfortunately, a lack of light-sensitive paper and plastic dishes at the time precluded taking the extra set of measurements.

Canopy openness (and other measures) was only measured at time 0 for MPF and SAF, and at time 0 plus soon after trees were felled, in GPF plots. For the purposes of this study, it was assumed that the light environment in plot types remained constant over 15 months. In reality, many small-scale changes would have occurred. For example, at the 15-month re-census in one MPF plot, most quadrats had not grown appreciably but the two quadrats in which plants had grown were near a disintegrating small tree that was allowing light to increase slightly overhead (or laterally). Also, high drought-induced leaf defoliation may have increased light levels in the forest plots. It would be hard to pinpoint which stage of change in the light environment the plants had responded to in these cases because they were gradual processes and began at unknown dates within the year. Furthermore, even if I had taken canopy openness measurements (the only light measure that was used in all quadrats) again, say at three and 15 months, the resolution of a spherical densiometer is not fine enough to detect such subtle changes over time (see pp.113-115). Hence, at the resolution that light was measured, my assumptions of constant light over 15 months were probably reasonable. MPF would have remained similar, and SAF would have decreased in openness but would still have been considerably more open than the forest plots. Changes to canopy openness in GPF quadrats that were heavily debris-laden may have been detectable over 15 months as the debris decomposed, but other quadrats would not have changed appreciably. The strength of quadrat-level

analyses among seedlings may have been improved if light had also been measured at 15 months and/or if hemispherical photographs had been taken in all quadrats.

8.3.2 Litter

The artificially created gaps caused little root-zone change because trees were felled, not uprooted (except for a secondary tree that was knocked over in one plot), so soil changes should have been minimal. Leaf litter cover stayed at similar levels in both MPF and GPF over the first three months. This was largely because ~90 % of all quadrat space available for litter deposition, that is, excluding rocks and large buttressed roots, was already covered at time 0.

Litter depth in both MPF and GPF increased during the three months of the drought as trees lost more leaves and litter decomposition rates were perhaps slower in the dry conditions. This parallels litter deposition in tropical rainforests that have pronounced dry seasons: maximum litter depth is at the end of the dry season (Molofsky & Augspurger 1992). In field observations, litter type seemed important: *Clinostigma* palm fronds and to a lesser extent, large *Campnosperma* and *Myristica* leaves, were thick and decomposition appeared to proceed slowly, particularly in the drought, but even under normal rainfall.

Mean litter depth was significantly greater in MPF than SAF at time 0, but by 15 months, SAF depth had increased so that differences were no longer significant (Figure 7.8). SAF did not strongly increase in litter depth during the drought as the forest plot types did, presumably because the lower living-biomass amounts and the better plant survival in SAF (see sections 8.4.2 and 8.4.3) meant that fewer plants defoliated and contributed to litter. SAF depth increased 3-15 months concurrently with shading over of open grassy areas by taller ferns and fast growth (then sometimes death) of existing and newly recruited early-successional trees and shrubs.

8.4 Plant responses among plot types over 15 months

I examined plant regeneration after natural and human-induced disturbance by comparing plant species composition, new recruitment, growth, health, and survival of woody species in mature-phase forest, gap-phase forest and sakau-agro forest. Table 8.1 highlights the regeneration preferences of common woody species and their status in each plot type.

8.4.1 New recruitment

The total number of new recruits was significantly greater in GPF than MPF and total recruitment per forest plot increased with increasing mean canopy openness. This effect of gaps is noticeable in other forests (e.g., Lawton & Putz 1988; Luizao et al. 1998; Hubbell et al. 1999). Nevertheless, new recruitment of seedlings in GPF generally mirrored what was already on-site at time 0 in the mature phase. The twenty most commonly present species barely changed in rank in MPF and GPF over 15 months (Appendix E). The two heaviest seed groups were far more abundant in MPF and GPF than seed-groups 3 and 4, at both time 0 and after 15 months. With the exception of *Campnosperma*, whose seedlings rarely survived from one census to the next, early-successional species (seed-groups 3 and 4) seldom recruited into the forest gaps. Seed-groups 2 and 3, and *Aglaia* and *Campnosperma* among individual species, recruited in significantly greater numbers to GPF than to MPF. Yet, seedlings of *Aglaia* and *Campnosperma* were already common in MPF at time 0 and were still among the top five woody species in both forest plot types at 15 months.

Light was the main measured factor affecting recruitment in the forest, but correlations depended upon the range of light conditions, that is, whether or not SAF quadrats were included. Within the forest, total recruitment (all species combined), as well as recruitment of seed groups 2 and 3 and *Clinostigma* (SD2) and *Campnosperma* (SD3) were positively correlated with light in forest plots and/or quadrats. Total seedling recruitment also increases with increasing light in Puerto Rican forest (Devoe 1990). In the Puerto Rican study, species with more massive seeds tended to recruit more with decreasing light. The present study on Pohnpei supports that result across the broad light range inclusive of SAF, but not necessarily

Table 8.1 Species ranks by standardised stem frequencies in each size-class over time

	SEEDLINGS (< 1.0 m height)						SAPLINGS (1-4 m height)				TREES (> 4 m height)			
Species rank	**Time 0**		**Total recruits**		**15 months**		**Time 0**		**15 months**		**Time 0**		**15 months**	
MPF 1	*Parinari*	522	*Parinari*	136	*Parinari*	472	*Parinari*	136	*Parinari*	136	*Clinostigma*	21	*Clinostigma*	22
2	*Aglaia*	201	*Campnosperma*	70	*Aglaia*	212	*Clinostigma*	20	*Clinostigma*	19	*Parinari*	17	*Parinari*	17
3	*Clinostigma*	162	*Clinostigma*	63	*Myristica*	87	*Aglaia*	18	*Aglaia*	19	*Cyathea*	7	*Cyathea*	7
4	*Myristica*	94	*Aglaia*	62	*Clinostigma*	65	*Pandanus*	9	*Pandanus*	9	*Garcinia*	4	*Garcinia*	4
5	*Campnosperma*	43	*Myristica*	40	*Campnosperma*	54	*Myristica*	8	*Myristica*	7	*Myristica*	3	*Myristica*	3
6	*Syzygium*	29	*Syzygium*	21	*Syzygium*	36	*Barringtonia*	6	*Barringtonia*	5	*Aglaia*	2	*Aglaia*	2
7	*Palaquium*	20	*Embelia*	11	*Palaquium*	25	*Cyathea*	6	*Cyathea*	5			*Barringtonia*	2
8	*Embelia*	19	*Palaquium*	9	*Embelia*	22	*Palaquium*	5	*Palaquium*	5				
9	*Cyathea*	14	*Discocalyx*	4	*Discocalyx*	15	*Glochidion*	2	*Glochidion*	2				
10	*Discocalyx*	13			*Pandanus*	11		7	*Canthium*	2				
Other spp.	10 spp.	28	9 spp.	9	12 spp.	28	7 spp.	7	6 spp.	6	10 spp.	10	9 spp.	9
Total stems		1145		425		1027		217		215		64		66
GPF 1	*Parinari*	491	*Campnosperma*	226	*Parinari*	478	*Parinari*	85	*Parinari*	76	*Clinostigma*	22	*Clinostigma*	20
2	*Clinostigma*	287	*Parinari*	140	*Aglaia*	247	*Aglaia*	24	*Clinostigma*	24	*Parinari*	11	*Parinari*	12
3	*Aglaia*	234	*Clinostigma*	126	*Campnosperma*	178	*Clinostigma*	21	*Aglaia*	22	*Aglaia*	4	*Aglaia*	7
4	*Myristica*	58	*Aglaia*	95	*Clinostigma*	127	*Pandanus*	16	*Pandanus*	16	*Myristica*	3	*Myristica*	3
5	*Campnosperma*	56	*Myristica*	25	*Myristica*	47	*Cyathea*	6	*Cyathea*	4	*Campnosperma*	2	*Pandanus*	3
6	*Syzygium*	24	*Syzygium*	8	*Syzygium*	27	*Myristica*	5	*Myristica*	4	*"kehtol"*	2	*Campnosperma*	2
7	*Embelia*	23	*Embelia*	8	*Embelia*	24	*Barringtonia*	2			*Pandanus*	2	*Garcinia*	2
8	*Pandanus*	13	*Palaquium*	3	*Palaquium*	13							*"kehtol"*	2
9	*Cyathea*	13	*Ficus*	3	*Pandanus*	11							*Cyathea*	2
10	*Palaquium*	11	*Pittosporum*	3	*Cyathea*	8								
Other spp.	7 spp.	8	6 spp.	9	11 spp.	21	4 spp.	4	3 spp.	3	6 spp.	6	4 spp.	4
Total stems		1218		646		1181		163		149		52		57
SAF 1	*Aglaia*	86	*Campnosperma*	133	*Aglaia*	102	*Cyathea*	54	*Cyathea*	73	*Clinostigma*	8	*Campnosperma*	17
2	*Melastoma*	74	*Aglaia*	35	*Campnosperma*	88	*Campnosperma*	50	*Melastoma*	68	*Campnosperma*	6	*Cyathea*	16
3	*Campnosperma*	66	*Cyathea*	13	*Cyathea*	32	*Melastoma*	40	*Campnosperma*	33	*Cyathea*	4	*Clinostigma*	7
4	*Cyathea*	54	*Myristica*	8	*Morinda*	22	*Parinari*	16	*Pandanus*	19	*Hibiscus*	2	*Barringtonia*	4
5	*Parinari*	23	*Melastoma*	4	*Parinari*	22	*Aglaia*	13	*Parinari*	19			*Cananga*	2
6	*Morinda*	22	*Morinda*	4	*Melastoma*	15	*Pandanus*	6	*Clinostigma*	16			*Macaranga*	2
7	*Clinostigma*	17	*Fagraea*	3	*Myristica*	13	*Clinostigma*	5	*Aglaia*	11				
8	*Barringtonia*	14	*Psychotria* sp. 1	3	*Psychotria* sp.1	13	*Barringtonia*	3	*Barringtonia*	4				
9	*Fagraea*	13	*Parinari*	3	*Barringtonia*	11	*Cananga*	3	*Cananga*	3				
10	*Ficus*, *Pandanus*, *Psychotria* sp.1	33			*Ficus*	11	*Claoxylon*, *Macaranga*, *Piper* sp. 2	6	*Claoxylon*	3				
Other spp.	13 spp.	48	9 spp.	13	17 spp.	53	4 spp.	4	6 spp.	6	6 spp.	6	4 spp.	4
Total stems		450		219		382		200		255		26		52

among forest plots and/or quadrats alone. For example, seed group 2 recruited more into higher light forest plots, but the overall light range in the mature- and small-gap-phase forest was narrow. Over the greater range inclusive of SAF quadrats, recruitment of the two heaviest seed groups was more numerous in lower light quadrats. Conversely, the lightest seed group was more abundant in its recruitment in higher light quadrats.

Despite personal observations about the effects of palm fronds and litter depth on new recruitment, neither litter depth nor volume, nor debris cover were important in Spearman's correlations with new recruitment frequencies, with the exception of *Cyathea* (recruitment frequencies were negatively correlated with litter depth). The deposition of palm fronds was highly variable, however, so although a large frond may strongly affect the survival of newly recruited seedlings covered by it, the effect is localised. Such local effects are probably drowned out in the present study because litter was estimated across a one-square-metre quadrat, and many other interacting micro-environmental and plant variables were uncontrolled. Litter depth was thicker and drier in forest quadrats during the drought so seedling establishment was presumably more difficult for the smaller-seeded species (litter usually negatively affects germination of small-seeded species - Molofsky & Augspurger 1992). Had gap initiators been uprooted in GPF plots – as appears to be most common in Pohnpei's forests – the upturned root plate would have provided more shallow-litter sites for small-seeded species to recruit.

Among the five most abundantly recruited tree species in MPF and GPF (see Table 8.1), *Clinostigma* and *Campnosperma* were common members of the mature-forest seed rain (Winthrop 1998). The seed rain study rarely caught *Parinari* and *Myristica*, but the seed trap design may have reduced the chances of large seeds being caught (ibid.). Surprisingly, however, Winthrop identified no *Aglaia* seeds in her seed-rain study in Pohnpeian MPF and SAF. Even if *Aglaia* were one of the species that she could not identify to family, unknown species were numerically scarce. Yet, my results show that *Aglaia* is managing to recruit well and survive in both SAF and forest plots. Perhaps *Aglaia* was not fruiting at the time of Winthrop's (1998) study since it covered only one collection period. *Aglaia* was not found in the seed bank either (Gardner 1997), but this was expected.

Parinari, *Aglaia*, *Clinostigma* and *Myristica* were all present as seedlings through to adult trees in MPF and GPF, and recruited in similar proportions to their

initial stem-frequency ranks (Table 8.1). In contrast, *Campnosperma* was present in MPF only as large trees or small seedlings. It recruited in disproportionately large numbers in MPF and especially GPF, but almost none survived between censuses. *Cyathea* was present as saplings and trees but rare as seedlings. This suggests that conditions in some areas of the forest were suitable for successful *Cyathea* or *Campnosperma* recruitment in the past but that these conditions are present no longer. The few newly recruited *Cyathea* seedlings in the forest were correlated not with light but with quadrats containing lower litter volumes.

SAF is undergoing successional changes in its species composition and structure. Presence of most species in SAF quadrats changed little over 15 months, but *Paspalum conjugatum* dropped in rank considerably, as did Vine 1. These two species prefer very open sites (Figure 6.13) that are presumably becoming more shaded. Similarly, in regenerating large gaps in Indonesia, Riswan and Kartawinata (1991) recorded *Paspalum conjugatum* dying out as early-successional trees grew and shaded the grasses. Recruitment frequencies of the short-lived early-successional *Melastoma* shrub in SAF was disproportionately low for its initial seedling ranking; it too is a species found in the most open SAF sites. *Campnosperma* and *Cyathea* were regenerating the most extensively in SAF. In contrast to its presence in the forest, *Cyathea* is common in all life-history stages in SAF. Recruitment of these two species was high, increasing their relative seedling ranks, and fast growth brought rapid transit through the seedling size-class and into saplings and larger trees. In contrast, *Parinari* and *Clinostigma* recruitment was very low in SAF, reflecting the remnant and isolated presence of these two species in SAF. *Parinari*, the most abundant and widely present of all species in the forest, did not even rank in the top twenty species for presence in SAF. *Clinostigma* also recorded few new recruits in SAF, but the seedlings present at time 0 grew rapidly so that many grew into the sapling size-class. Both *Clinostigma* and *Parinari* were more common in the higher size classes than as seedlings, further illustrating their remnant status, like *Cyathea* in MPF and GPF. Clearly, present conditions in SAF are excluding late-successional species.

8.4.2 Health

Woody-debris cover in GPF quadrats increased from less than 1 % to over 10 % of quadrat area between time 0 and 1 month while MPF cover remained largely

constant. The woody debris in GPF increased physical damage among GPF seedlings and saplings slightly by the three-month recensus. This was particularly noticeable in seed-group 1 species (*Parinari* and *Myristica*) because the persistence of their advance-growth seedlings made them available for damage over a longer period. Long-persisting juveniles of late-successional species, like *Parinari*, may be damaged more frequently than earlier successionals because they occur under and tolerate greater canopy cover, and grow relatively slowly so remain longer in the smaller size classes (Aide 1987; Clark & Clark 1991). In theory, once a gap has formed, physical damage to seedlings and saplings within a gap is less than in mature forest because less crown biomass is available overhead in a gap to fall (Clark & Clark 1991). For this reason, physical damage as a proportion of gap area can be less in large gaps than in small ones (Putz & Brokaw 1989). However, I followed plants through the gap process rather than just studying them after gaps were created; hence the greater physical damage recorded in gaps than in mature forest. Gap initiators sometimes damaged censused plants when they fell, but all residual individuals and debris remained on site. Plant health was measured only for three months, so I do not know for how long gap debris affects GPF health. Reduced plant health may prove to be only temporary and physical damage may be less in future, as theory would suggest. Nevertheless, damage caused when GPF gaps opened likely contributed to GPF's greater seedling mortality than in MPF (see mortality section 8.4.3). Physical damage recorded at the initial census among plot types was associated with reduced 15-month seedling survival in the time 0 cohort for seed-groups 1 and 2. Biotic cover was also an important influence on seedling mortality for seed-group 1. This may be a direct influence or it may correlate for age or slow growth in the long-persisting, advance-growth seedlings (see Figure 8.2a vs. 8.2b).

Many *Aglaia* and *Parinari* seedlings and saplings re-sprouted after physical damage like bent stems, snapping or die-back of the central leader, or broken branches. These two species have large advance growth populations, so the ability to re-sprout allows their advance growth to recover from physical damage associated with Pohnpei's many small disturbances and then successfully compete for any increased above- and below-ground resources. Juvenile sprouting will also increase the chances of advance growth surviving and successfully responding to rare but large typhoons that can hit Pohnpei, just as sprouting does elsewhere after hurricanes (Walker 1991; Yih et al. 1991; Bellingham et al. 1994). Note that I only observed re-sprouting in

juveniles so I do not know whether adult trees of *Parinari* and *Aglaia* can re-sprout after severe damage. The only adult re-sprouting that I did record was a *Barringtonia racemosa* (L.) Spreng. after it was felled previously in a SAF plot.

For most species, SAF health was the highest of all plot types. Biotic cover on both seedlings and saplings in SAF was much lower than in the forest plots. This may have resulted from the much higher light conditions in SAF because higher light areas are thought to be less conducive to pathogens (Augspurger 1984b). High light also promoted relatively rapid plant growth, especially for early-successional species, so plants transited through the size classes faster in SAF and, therefore, were exposed to juvenile infection and predation for a shorter time. Note that high biotic cover as recorded in this study does not necessarily mean that plants are damaged because the non-health code included the possibly benign epiphyll cover as well as the more detrimental fungal growth and insect attack. Nevertheless, as mentioned before, more of the time 0 cohort of seed-group 1 seedlings that died over 15 months were biotic covered than those that survived.

Saplings, presumably by their greater age compared to most seedlings, were less often classed as healthy than seedlings. Conversely, biotic agents affected saplings considerably more than seedlings, in much the same way as *Parinari* seedlings were classed as healthy less often than species like *Clinostigma* and *Campnosperma* because of *Parinari*'s persistence. Physical damage in GPF post-gaps increased equally for seedlings and saplings.

8.4.3 Mortality

In all plot types, seedling mortality was vastly greater than saplings and larger trees, as is common in other forests (Clark & Clark 1992; De Steven 1994). In general, seedling mortality related to plant size, that is, the larger the seedling, the longer it survived, a result other researchers have found (Sarukhán 1978; Turner 1990b; Brown & Whitmore 1992; Still 1996). Brown and Whitmore (1992) suggested that small seedlings have higher mortality, in part, because they have fewer leaves and less developed root systems to enable survival from desiccation and photosynthetic shock when gaps open.

Survival of pre-existing plants is often much higher than new recruits (Uhl et al. 1988; Brown & Whitmore 1992; Thompson et al. 1998). Similarly in my study,

seedling mortality between three and fifteen months was much greater for the newest recruits (i.e., from the three-month recensus) than older recruits or the time 0 cohort. Age- and size-dependent mortality interact since, as was found in the present study, at a particular time, seedlings from older cohorts tend to be taller than those from younger cohorts.

Tree and shrub mortality patterns varied among species and seed-groups in both drought and non-drought periods, just as other authors have recorded, even among closely related species (e.g., during droughts: Leigh Jr et al. 1990; Condit et al. 1995; Nakagawa et al. 2000; non-drought periods: Turner 1990b; Welden et al. 1991; Brown & Whitmore 1992; Still 1996). Among common tree species in the forest, *Parinari* seedling mortality was the lowest, and *Clinostigma* and especially *Campnosperma* were the highest. Species differences were attributable to seedling size and, consequently, size-dependent mortality (see above), as well as successional status. The majority of *Clinostigma* and *Campnosperma* seedlings grow initially to less than 20-cm height compared with about 50 cm for *Myristica* and 60-100 cm for *Parinari*. Hence, the taller seedlings of *Parinari* (and *Myristica*) had greater survival than the species with smaller seedlings. Nevertheless, even among species with similar-sized seedlings, survival in forests was considerably greater for *Aglaia* than *Clinostigma*, and lowest for the early-successional *Campnosperma*. Other early-successional species common in SAF are relatively short-lived, such as *Melastoma*, and showed rapid height growth followed by high sapling death.

Health results reflected the different mortality rates among species. For example, the heavy-seeded *Parinari* produced large advance-growth seedlings that survived longer than seedlings of other species, including during the drought, and thus had more time to become bent, eaten by insects, or infected by pathogens. The health of *Parinari* seedlings reflected this persistence; seedlings were more bent and biotic-covered than most other species. In contrast, both *Campnosperma* and *Clinostigma* recorded high proportions of healthy individuals but that was largely because few seedlings survived beyond early establishment.

Seedling mortality was lowest during the three censused drought months in SAF and tended to be highest in GPF. The reasons underlying these drought mortality patterns relate to differences among plot types in micro-environmental conditions as well as species presence and size-class distributions.

1. Differences in woody species composition among plot types

For trees and shrubs, early-successional species such as *Campnosperma*, *Cyathea*, *Melastoma*, and *Morinda* dominated SAF, whereas late-successional species were far less common. Conversely, the forest was dominated by late-successional species and had few early-successional species. Late-successionals such as *Syzygium*, *Garcinia*, and *Palaquium* were absent from SAF plots, while *Parinari* and *Clinostigma* were not nearly the dominant species in SAF that they were in the forest. The early-successional *Campnosperma* was common in all plot types, but survival in GPF and MPF was abysmal; only in SAF did its seedlings survive and grow. Therefore, as early-successional species tend to be adapted to more open and drier sites, the species assemblage in SAF was better pre-adapted to surviving the drought than species in the forest.

2. Species size-class distributions in plot types

Even among individual seed-mass groups and species, SAF seedling mortality was lower during the drought. In particular, SAF mortality was lower for all seed-mass groups as well as *Parinari*, *Campnosperma*, *Clinostigma*, and *Cyathea* among common species. Species strongly affected by the drought in forest plots such as *Clinostigma* and *Campnosperma* tended to be taller in SAF than in MPF or GPF. This was because SAF's high light conditions enhanced seedling growth and, in *Clinostigma*'s (and *Parinari*'s) case, new recruits were rare. At three months, the percentage of seedlings 25-100 cm (as opposed to small seedlings ≤ 25 cm) for *Clinostigma* and *Campnosperma* was 24 % and 0 % in MPF, 10 % and 0 % in GPF, and 47 % and 15 % for SAF. As mentioned above, survival results of the time 0 cohort showed that irrespective of the plot type, taller plants survived longer than shorter ones, most likely because their greater number of leaves and more developed root systems decreased desiccation stress (Brown & Whitmore 1992). Hence, seedling survival of several common forest species was higher in SAF because a greater proportion of those individuals was taller in SAF. Note that the drought may have been so severe on many species, particularly those with small seedling heights that even larger seedlings died in the drought. Initial heights of *Campnosperma*,

Clinostigma, and *Aglaia* seedlings that died by three months were higher than those dying by 15 months.

3. Different micro-environments among plot types

The SAF physical environment was more open than the forest both before and after the drought. Large gaps like sakau plots have higher maximum air and soil temperatures and lower relative humidity than in closed-canopy forest (Whitmore et al. 1993). Therefore, seedlings of any species that survived germination and establishment in SAF may have already adapted physiologically to those conditions and so were better adapted to survive when the drought came than seedlings present in the forest. Within the forest, GPF mortality was higher than in MPF during the drought, probably because water stress came just after gaps opened, accentuating initial changes after gaps were created, for example, in microclimate, pathogens in decaying debris, or competition. Hence, even though SAF normally represents a more extreme environment for later-successional species, the drought subjected existing individuals in GPF to the most stress because initial gap conditions exacerbated the effects of the drought. This follows research in Malaysian forest where seedlings in new gaps initially were hit harder by a drought (Turner 1990a). Also, in Panamanian forest, which experiences a regular dry season, a severe El Nino drought (1982-83) was more keenly felt by species that normally occurred preferentially in wetter micro-habitats during the dry season (Condit et al. 1996). The authors presumed that such species were less able to tolerate drought stress than species typically living in dry sites in the dry season.

Post-drought seedling mortality (relative to the previous census total) was slightly but consistently greater in GPF than in MPF, but was only significant for seed-group 2 species, particularly *Aglaia*, from three to fifteen months. In contrast, other authors have found seedling mortality to be generally lower in gaps than in the more-shaded mature forest (Augspurger 1984b, 1984a; Brown & Whitmore 1992; Kennedy & Swaine 1992; Thompson et al. 1998), although for Turner (1990b), seedling mortality was not correlated with light. The reported benefits to young seedlings establishing in gaps, for example, reduced pathogen attack (Augspurger 1984b), may not have been significant factors in my gaps because changes in light conditions from mature to the gap phase were subtle (see section 8.3.1). Also, Augspurger (1984b)

used transplanted seedlings in gaps whereas in the present study the initial cohort of seedlings had to survive gap creation *in situ* and, consequently, some were physically damaged. Survival of advance growth was equally high in both gaps and closed forest in a study by Uhl et al. (1988).

Part of the greater mortality in GPF will relate to differences in species recruitment between MPF and GPF. Greater new-recruitment in GPF compared to MPF skewed the GPF size-class distribution more towards smaller seedlings so size- and age-dependent mortality was felt more amongst the abundant newly recruited small seedlings in GPF. Mortality rates for *Campnosperma* were similar between MPF and GPF because virtually all seedlings died within weeks of germinating in either forest condition. Only in SAF did *Campnosperma* seedlings survive.

The higher seedling density recorded in GPF than in MPF had the potential to cause some density-dependent mortality in GPF. Results indicate, though, that most mortality was among species with small seedlings and/or species that can least tolerate the low-moderate light conditions found in GPF, such as *Campnosperma.* For example, limited dispersal opportunities resulted in a high density of *Parinari* seedlings establishing under conspecific adults. Yet, their survival was considerably greater than species like *Clinostigma* and *Campnosperma* because of their larger seedling size.

Among all plot types, post-drought seedling mortality was lower in SAF than in either MPF or GPF for seed-group 1, *Parinari*, and *Campnosperma,* and similar for groups 2 and 3, *Aglaia*, and *Clinostigma.* Mortality in seed-group 4, including *Cyathea*, was greater in SAF than in MPF or GPF. This was mostly because *Cyathea* occurred in the forest as larger individuals and had few new recruits, so mortality, again size-dependent, was lower in the forest plots than in SAF.

8.4.4 Height growth

Changes in mean seedling height over 15 months in MPF and GPF were partly artefacts of mortality and new recruitment patterns among species. Forest heights increased initially (to three months) because the drought mortality was very high (Figure 7.9), and was concentrated in small-seedlings (see Section 8.4.3), while new recruitment was low. Mean height at 15 months was lower than at one and three months because mortality had decreased while new recruitment had increased. In

contrast to the forest plots, mean height over time in SAF was lower at three months than at time 0 and decreased again slightly by 15 months. This was because drought mortality was slightly lower than recruitment 1-3 months and when mortality did increase 3-15 months, new recruitment helped to balance it. Also, seedling growth was rapid in the SAF plots so many seedlings moved from the seedling class to the sapling class (see Figure 7.15b).

Height growth in GPF tended to be greater than in MPF for all subgroups and species, and was significantly greater for large- and small-tree species and seed-mass group 2, as well as individually for *Aglaia.* This trend conforms to gap-phase theory and studies showing that plants grow more in the higher light of gaps (e.g., Uhl et al. 1988; Turner 1990b; Fraver et al. 1998; Luizao et al. 1998). Nevertheless, fifteen months is not long in the life cycle of rainforest plants; even in GPF, mean absolute height growth 0-15 months was only a few centimetres for most species. Similarly, in Malaysian forest, seedlings grew more in gap sites than closed-canopy sites but plants generally grew only a few centimetres in 16 months (Turner 1990b). Plant growth in SAF was considerably higher than in the forest plots, with a few plants of early-successional species growing almost three metres in 15 months. Among the three plot types, seedling growth was highest in SAF for seed groups 3 and 4, but growth of seed-group 1 and 2 species tended to be similar or higher in GPF than SAF.

Generally, height growth increased with increasing light. However, this relationship differed among seed-mass groups and species and was dependent upon the analysis scale (plots vs. quadrats), sample size, and the range in light conditions. For example, plot-mean absolute (and proportional) height growth 0-15 months related significantly to mean canopy openness for all species combined and for seed-groups 1 and 2, for MPF and GPF plots alone as well as all plots together. Seed-group 3 and *Parinari* growth related to light only when SAF plots were included, presumably because of the extended light range, and for seed-group 3, the greater seedling presence. Growth of seed-group 4 was not correlated with light at the plot-level but was correlated quite strongly at the quadrat level. In contrast, the growth-light relationship for other seed groups was weaker at the quadrat level than among plots, even when compared to the site factors from hemispherical photographs, reflecting the greater variability among quadrats than among plots. Likewise, Turner (1990b) found that a seedling growth to light (direct-site-factor) relationship for Malaysian *Shorea*

species in one-square-metre sample units (the size of my quadrats) was weak or non-existent.

Proportional height growth of the time-0-seedling cohort tended to be greater over 15 months the lighter the seed-mass group, except for seed-group 3 in MPF and GPF (Table 7.21). This conforms to the tendency of species adapted to higher light to have greater plasticity and acclimation than shade-tolerant species, so they generally grow faster and also adapt growth faster when conditions change from shade to higher light (Denslow et al. 1990; Bazzaz 1991). Differences in absolute and proportional height growth among seed groups were greatest in SAF and most restricted in MPF (Table 7.21). This reflects the generally positive growth response of species to light that resulted in SAF seedlings growing considerably more than seedlings in MPF (Table 7.21). It also supports Boot's (1996) results from Guyana's forests that species-specific differences in relative growth rate are quite small in shaded environments but increase with increasing light. In the present study, differences in growth rates among seed groups, even within a particular plot type, related in part to species presence since, among quadrats, seed-group 3 and 4 species occurred predominantly in higher-light quadrats whereas seed groups 1 and 2 occurred in more shaded quadrats. Nevertheless, even when light among quadrats was accounted for in an ANOVA model, growth still tended to be greater among the light-seeded species, but only seed-group 4 grew significantly more than the other seed groups.

Where a species grows best is not necessarily where it competes best and therefore occurs most. Although seedlings of seed-groups 1 and 2 grew more in higher light plots so growth was higher in SAF and GPF than in MPF, their seedlings were seldom present in SAF. This was due to the weeding of advance growth, a lack of new seeds (Gardner 1997; Winthrop 1998), strong competition from non-woody species, and perhaps desiccation and photo-inhibition of seeds and seedlings.

Absolute and especially proportional seedling height growth 3-15 months tended to be greater for younger plants (Table 7.24, Appendix I), especially for *Parinari*, and growth of newly recruited *Parinari* decreased with increasing initial height (Figure 7.17). These results are contrary to research showing that growth is greater for older individuals (Brokaw 1985a, saplings), and larger seedlings (tropical: Uhl et al. 1988; Brown & Whitmore 1992; temperate: Orlander & Karlsson 2000). Nevertheless, the results support findings in some temperate forests that growth rates

decrease with increasing plant age and/or size (Hatcher 1964; Ferguson & Adams 1980; McClure et al. 2000).

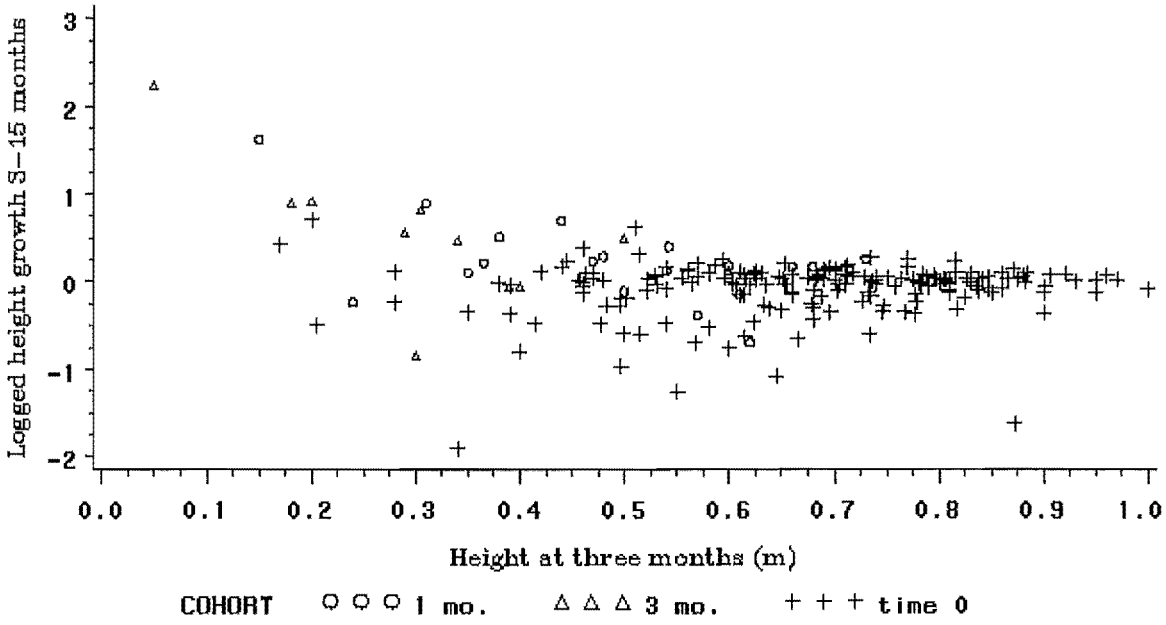

Figure 8.1 Logged, quadrat-mean height growth 3-15 months vs. initial size, by recruitment cohort, for *Parinari*.

Growth differences among the cohorts may not last long; I followed plants for only a maximum of 15 months, depending upon the cohort. Indeed, for *Parinari* and probably other very large-seeded species, younger seedlings were initially smaller but grew faster in their first 12-14 months because, most likely, they were living off maternal allocations in the seed endosperm. When 3-15 month growth is graphed against initial height for *Parinari*, the slope is negative to 40-50 cm height, then flat (i.e., no relationship) for the larger individuals (Figure 8.1). Thus, the seed reserves lift the new seedlings to 50 cm, but once they have to rely on the abiotic environment, usually in deep shade for *Parinari*, their growth slows and so begins their advance-growth persistence. Among the time 0 cohort, growth over 15 months was not significantly related to initial seedling size for any seed group. Also, among seed groups, proportional height growth 3-15 months for new recruits was greater for species with heavier seeds (Table 7.24). This was the opposite trend to older seedlings in the forest: growth among the time 0 cohort over 15 months was generally greater the lighter the seed mass. Young seedlings grew fast initially from their seed reserves, and heavier-seeded species, which have more food reserves than the lighter-seeded species, grew faster initially than lighter-seeded species.

Plants were followed for 15 months, but I would predict that growth in GPF and MPF will diverge more in the year or two following my last measurements. A few seedlings and saplings will continue to grow rapidly in GPF, and older advance growth, whose growth responses to the new microclimate can be delayed compared to younger advance growth (Hatcher 1964; Ferguson & Adams 1980), adjust positively in quadrats where light-levels have increased. Nevertheless, gaps are transient. Small gaps begin to close within a few months and can mostly close over again within about four years (Luizao et al. 1998). Uhl et al. (1988) found that growth in small Venezuelan gaps was greater in the first two years after gap formation than in the next two years as gaps aged and light availability decreased. Consequently, growth differences between my small gaps on Pohnpei may continue to diverge from MPF for only about two more years. Similarly, SAF growth rates may converge closer to those of GPF in the following few years as a low canopy of early-successional trees develops and canopy openness at the seedling level decreases.

Although I delineated three plot types in this study, all the plots formed a continuum of disturbance with respect to height growth. For example, SAF plot 5 was often closer to GPF than to SAF in seedling discriminant analyses. This plot retained more remnant large trees during sakau cultivation than the other SAF plots and, once abandoned, had noticeably more regenerating trees and shrubs and less non-woody species coverage. Plot 5's mean canopy openness at time 0 was 14 % compared to over 25 % in each of the other SAF plots. Like sakau plot 5, GPF plot 7 was mis-classified in discriminant analyses, as MPF. Over half the quadrats in GPF plot 7 became darker after gap creation because the *Parinari* tree crown fell near the plot.

8.5 The role of advance growth in forest regeneration patterns

The likely establishment mechanism(s) used by 20 commonly recorded tree and shrub species are presented (Table 8.2)[18]. Results of presence and abundance of species at time 0, their new recruitment, growth, and survival, plus information on seed

[18] I have excluded the role of sprouting as an establishment mechanism because data are lacking for Pohnpei. However, it is noted that elsewhere sprouting is very important for regeneration, after both small-scale- (Arevalo & Fernandez-Palacios 1998) and large-scale disturbances (Walker 1991; Yih et al. 1991; Bellingham et al. 1994).

rain (Winthrop 1998) and the soil seed bank (Gardner 1997) were used to gauge species' establishment strategies.

Common tree and shrub species with heavier seed masses (groups 1 and 2: average dried seed masses of 0.1 g or more) established from advance growth and seed rain and almost never from the soil-seed-bank (Table 8.2). Conversely, species with lighter seed masses (groups 3 and 4) arrived through seed rain and the soil seed bank but not through advance growth. Similar patterns have been found in Puerto Rican forest (Devoe 1990) and in Mexico (Martinez Ramos & Soto Castro 1993). It is not surprising that establishment via advance growth and seed banks are almost mutually exclusive since they represent the same type of strategy - persistence through semi-dormancy - but they operate at different life-history stages.

Table 8.2 Regeneration strategies of common tree and shrub species.
√= species uses this establishment mechanism, P= probable use of this mechanism, ?= possible use of this mechanism, X=species does not use this establishment mechanism. Sprouting ability not included.

Species	Advance growth	Seed rain	Soil seed bank	Seed mass group
Parinari	√	√	X	1
Barringtonia	P	√	X	1
Myristica	√	√	X	1
Syzygium	√	?	X	2
Clinostigma	√	√	X	2
Aglaia	√	√	X	2
Discocalyx	√	?	X	2
Palaquium	√	?	X	2
Pandanus	P	P	X	2
Cananga	X	√	P	3
Macaranga	X	?	√	3
Embelia	?	P	?	3
Campnosperma	X	√	√	3
Morinda	X	√	√	3
Claoxylon	X	P	P	4
Ficus	X	√	?	4
Melastoma	X	√	P	4
Cyathea	X	√	?	4

On Pohnpei, seedlings and saplings of seed-groups 1 and 2 were statistically associated with both MPF and GPF at time 0 and 15 months and seedlings were more numerous in quadrats (all plot types combined) as light levels declined. Stem frequencies of seed group 3 (intermediate seed masses) were statistically associated with SAF at time 0, but new recruitment was associated more with GPF. Across all quadrats, seed group 3 frequencies at time 0 as well as new recruits were not correlated with light, but in forest quadrats alone, recruitment was greater in higher light. *Campnosperma*'s (SD3) abundant recruitment in all three plot types, and greatest recruitment in GPF rather than SAF (Table 7.13), was uncharacteristic of strict definitions for early-successional/pioneer species (sensu Swaine & Whitmore 1988). However, seed supply of *Campnosperma* to SAF was limited: *Campnosperma* contributed a smaller proportion to the seed rain and was less widely dispersed in SAF than in MPF (Winthrop 1998). Furthermore, virtually all *Campnosperma* seedlings died shortly after recruitment in both MPF and GPF, so its regeneration results in the forest were superficial; generally, only seed groups 1 and 2 established and survived in small tree-fall gaps. Species with the lightest seed masses (SD4) were more numerous in quadrats as light levels increased and were associated with SAF.

Advance growth and seed rain, therefore, are the dominant mechanisms by which woody species successfully regenerate following small-scale disturbance in Pohnpei's upland forest. Conversely, recruitment from seed rain and the soil seed bank dominate establishment in the higher light areas of SAF. These results conform to ecological expectations about the typical establishment mechanisms and preferred environments for species near the poles of the successional gradient (Whitmore 1975, summarised in Chapter Two, p.18, of this thesis).

Results from my study among the later-successional species show that while these species all utilise the advance-growth mechanism to regenerate, they vary widely in the extent of their use (c.f. regeneration characteristics of *Parinari* vs. *Clinostigma*, next section). Within seed groups 1 and 2, species differed in their seed mass, seedling size and morphology, as well as adult height and canopy architecture, tolerance of shade-suppression, and growth rates in low-moderate light conditions. In addition, within a species, the time of establishment influenced later growth and survival.

During the study, taller seedlings generally survived longer than shorter seedlings, and the advance-growth/time 0 cohort survived longer than new recruits. Older seedlings were also taller; at 15 months, mean seedling height was always

greatest for the advance-growth than for newer recruits (Appendix J). In contrast to survival, new recruits tended to grow more in 12 months than the advance-growth seedlings, although this depended upon the species (Table 7.24, Appendix I). Yet, evidently, faster growth by new recruits over 15 months was not sufficiently great to displace the initial height dominance of advance growth.

These results suggest that species balance survival against growth in their regeneration strategies. An individual present as advance growth when a tree falls has a sizeable survival advantage over individuals only just recruiting from seed. Furthermore, although their initial growth rates may not be as high as new recruits, advance-growth seedlings already have a large height advantage, especially for species such as *Parinari* and *Myristica*.

What is the probability that a younger plant, starting from scratch but growing faster, will reach the same height in the finite period of elevated gap-light conditions as the pre-existing seedling growing more slowly? This trade-off question between advance growth and new recruits is comparable to differences between early- and later-successional species. Boot (1996) simulated a trade-off between early- and later-successional species related to their establishment mechanisms. Assumptions were that, firstly, relative-growth-rate differences between successional statuses increased with increasing light; secondly, early-successional species have a similar or higher growth rate in all light environments; and thirdly, that late-successional species have larger seeds and seedlings than early-successionals. Under these conditions, which my results showed are generally valid for Pohnpeian forest, small seedlings of early-successional species took 691 days to reach the same size as a slow-growing but initially larger later-successional seedling in light conditions typical of small gaps. In higher light conditions, however, where growth differences are assumed to be greater, and were found to be on Pohnpei, it took only 86 days for the early-successionals to reach equal size. That is provided that the plants all survive, which may not be the case; survival chances in Pohnpei's forests were considerably lower for smaller and younger seedlings.

Boot's (1996) model demonstrates how individuals arriving at the time of or just after a small gap opens, whether they be earlier-successional species or new recruits of later-successional species, will not likely compete successfully against plants pre-existing as advance growth (almost always later-successional species). Hence, small-scale disturbances in Pohnpei's upland forest generally benefit advance

growth more than new recruits from seed rain, just as Uhl et al. (1988) found in Venezuelan forest. Nevertheless, small-scale spatial variability in litter and light within GPF and physical damage to advance-growth can provide a few opportunities for newly recruited individuals to establish, grow and survive, at least in the short term. For example, near the maximum-light centre of one GPF gap (but not in any censused quadrat) a *Campnosperma* established that was over 20 cm in height, which is above the usual death mark for *Campnosperma* in MPF and GPF. Whether this seedling survives long-term will depend upon how fast it grows before its overhead light levels are reduced as the gap closes. However, light levels in a small gap, such as those studied on Pohnpei, are rarely high enough to allow any individual, regardless of species or recruitment-cohort, to grow to adulthood before being suppressed by taller trees as the gap closes. Consequently, juveniles must go through a series of gaps opening and closing, and probably spend a large proportion of their lives moderately to deeply shaded, before reaching adulthood (Becker & Wong 1985; Brokaw 1985b; Uhl et al. 1988).

In contrast to small gaps and their low-moderate light levels, differences in growth rates amongst seed groups were greatest in the high light levels typically found in SAF (Table 7.21). Early-successional species grew much faster than later-successional species and dominated the SAF regeneration. In addition, a large-scale-disturbance event will increase physical damage to advance growth, disadvantaging them against fast-growing, newly recruited plants.

Thus, the physiology of later-successional species centres upon long-term survival because they mostly occur in shaded forest sites that limit growth and require juveniles to persist and adapt to a series of gaps opening and closing before reaching adulthood. As advance growth age, they may gradually lose their ability to adapt quickly to changes in the micro-environment around them. In contrast, earlier-successional species are physiologically more focused on growth than on long-term survival. If the light conditions are low and are consequently not conducive to rapid growth, seedlings do not persist until favourable conditions occur; they perish. A greater emphasis, therefore, is placed upon ensuring seeds are easily and widely dispersed and are present at or soon after large disturbances occur; then the seeds germinate and the seedlings grow rapidly. Transit through the seedling stage is much faster than for individuals as advance growth.

A species's advance-growth population is heterogeneous and dynamic. Seedling health may deteriorate gradually because persistence without appreciable growth exposes a plant to biotic and physical damage for a longer period. Reduced health affects survival: seedlings in this study that were classed as not healthy within the time 0 cohort were more likely to die. Younger seedlings in some species grew faster, at least initially, probably based on their seed reserves and greater physiological plasticity (see growth section, 8.4.4). Mortality of young seedlings in mature or small-gap forests is very high initially but tapers off considerably within a few months, depending upon the species. Therefore, relatively young advance-growth seedlings that have reached similar heights as the majority of advance-growth for that species might adapt most quickly to micro-environmental conditions in new small gaps than either seed-rain recruits, which are initially much shorter, or much older advance growth. This will depend not only upon the age and size of the individuals, but also especially on individual plant vigour prior to gap formation as estimated by, for example, the number of leaves (Ashton & deZoysa 1989) or growth rates (Hatcher 1964; Ferguson & Adams 1980). In addition, differences in growth between younger and older advance-growth seedlings may be less on fertile sites (Hatcher 1964).

Advance growth has been studied in more detail and longer term in temperate forests than in tropical forests. This is largely because the slower temperate growth rates necessitate long-term research, advance growth has long been used in Europe and North America for restocking natural forests after logging, and tree ages can be accurately determined from growth rings. In one such study in northern hardwood forest in USA, trees were tracked for approximately 45 years (depending on the plot) after large gaps were cut, and the stems analysed to determine the age of first establishment (McClure et al. 2000). The authors found that no stems surviving after 45 years had established later than four years after the gap opened. Furthermore, like my results, albeit after only 15 months (pp.136-137), species differed in the proportion of stems present that established prior to gap formation (i.e., advance growth) vs. those that established post-gap (new recruits). After 45 years, advance-growth comprised as low as 20 % of stems in the least shade-tolerant species, up to 75 % in more shade-tolerant species. Species differed in their average heights at gap formation, related to average age, the length of time before growth rates declined, and the length of time it took for new recruits to catch up with advance growth. New recruits of the most shade-tolerant (as juveniles) species caught up relatively soon (i.e., within 15 years).

For others, heights were similar after 30 years. For the least shade-tolerant species, advance growth juveniles were always taller than new recruits, even if they were only one or two years older. Like the results of McClure et al. (2000), the degree to which species' growth and survival results from my 15-month research are maintained in the long-term will vary among the species.

To illustrate differences among species' regeneration strategies along the successional gradient, I will discuss the regeneration characteristics of the three forest canopy dominants: *Parinari laurina*, *Clinostigma ponapensis*, and *Campnosperma brevipetiolata*.

Parinari laurina

Parinari laurina is a classic late-successional species. It is a forest dominant, forming a dense, leafy canopy, but is not an emergent. *Parinari* was the most abundant of all species in mature forest at time 0, including a large population of advance-growth seedlings and saplings. Remnant populations were present in some sakau plots; *Parinari* was the fifth most abundant species in SAF, but like *Clinostigma,* was narrowly dispersed. It has very large fruits, no seed bank presence (Gardner 1997), and is rare in the seed rain, although that may have been an artefact of seed trap design (Winthrop 1998).

Among all plot types, quadrat stem frequencies of *Parinari* at time 0 were strongly negatively correlated with light and non-woody cover. New recruitment of *Parinari* in quadrats was also correlated negatively with light (ISFC, DSFC and photo-papers at 1 m). Not only was this correlation due to *Parinari*'s strong shade preference for establishment, but with only gravity for dispersal, fruits mostly fall and germinate beneath their densely shading parent trees. I also observed that seedlings and saplings readily re-sprouted if bent over or snapped, a useful response when living in the dark forest understorey for a long time and subject to constant small-scale disturbance.

The tall height of *Parinari*'s advance-growth seedlings, 60-100 cm, affords them survival chances that are considerably better than other common tree species such as *Clinostigma*, *Algaia* and *Campnosperma* (see discussions on health 8.4.2 and mortality 8.4.3). Despite recruiting and competing better in lower light quadrats, seedling growth for *Parinari* correlated positively with increased light. Yet, a sudden increase in light through gap formation does not necessarily result in accelerated

growth for all. Theoretically, non-aplastic advance-growth seedlings can be old in age but are assumed to be capable of behaving like physiological youth of similar size when gap openings give them the opportunity to accelerate their growth (Oliver & Larson 1996, p.137). However, while some seedlings in newly illuminated GPF quadrats grew quite rapidly - as one might expect - others of similar size just sat there. These latter advance-growth may have persisted in a semi-suspended growth stage in deep shade for so long that they are incapable of quickly switching from a shade to sun physiology; hence, they can not accelerate rapidly, if at all, their growth rates when a gap opens. I could not specifically measure the age of advance-growth seedlings and saplings without a very long-term survey. Nevertheless, health results showing high biotic cover and physical damage on *Parinari* seedlings and saplings suggest that some of the advance growth may be quite old indeed (c.f. Figure 8.2a vs. 8.2b).

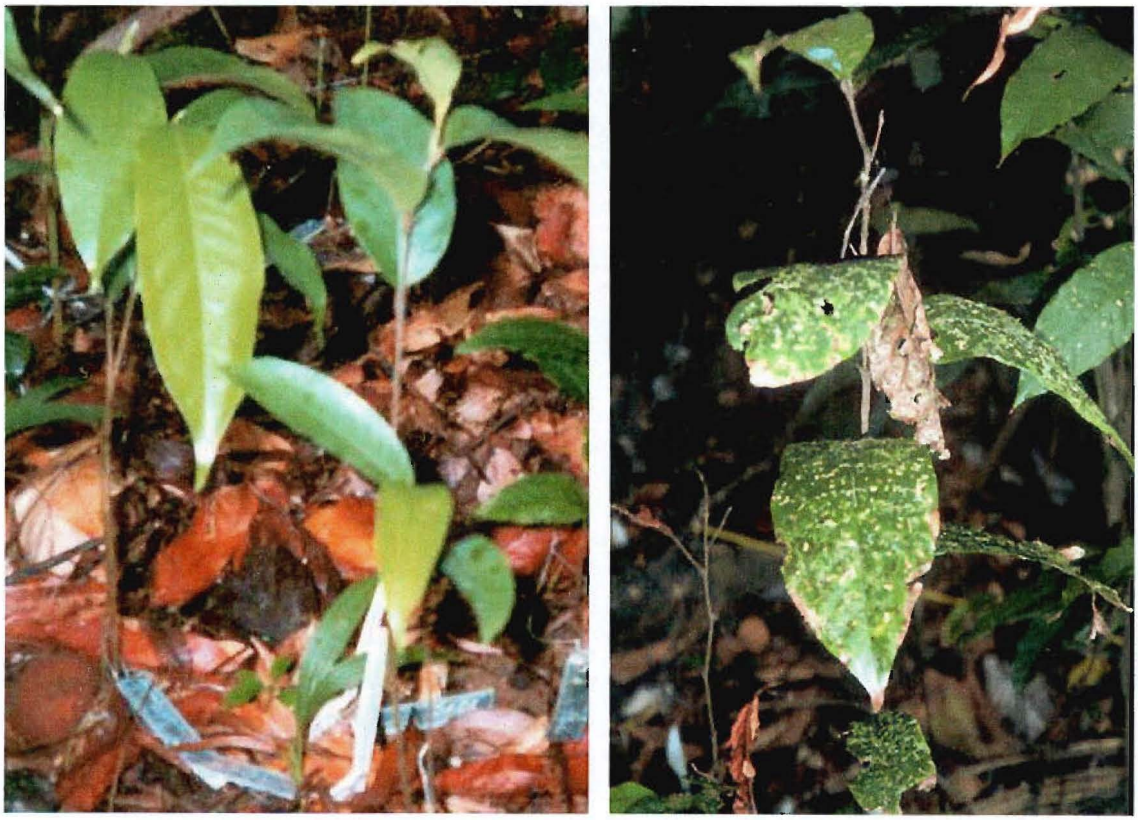

Figure 8.2 (photo): *Parinari* seedlings.
a) Newly recruited seedlings (less than one year old), and b) old advance growth (of unknown age).

Seedling growth among *Parinari* was age-specific between advance-growth and new recruits as well as size-specific among new recruits up to about 50 cm, but was not significantly size-specific within the advance-growth population alone.

Studies in temperate forests suggest that younger advance growth respond faster to enhanced light than older advance growth and, regardless of age or size, vigorous growth rates before a gap opens correlate with vigorous post-gap growth (Hatcher 1964; Ferguson & Adams 1980). Highly suppressed advance growth can take a number of years to respond significantly to elevated light levels (Ferguson & Adams 1980). Hence, of two similarly-sized seedlings, one might expect a younger advance-growth *Parinari* to respond better to elevated light conditions in areas of gap-phase forest than an old advance growth.

Whitmore (1989) classed a related species, *Parinari papuana* ssp. S*alomonensis*, as pioneer class 1, that is, a species that establishes and develops in high forest rather than canopy gaps. *Parinari laurina* is similar, but its growth is not aplastic. Seedlings sit as advance growth 60-100 cm in height, but then (at least some members of the advance growth) increase growth in relation to elevated light levels. Thus, *Parinari* is not indifferent to changes in light level; rather, its seedlings and saplings can persist for long periods in low light while seedlings of other species perish.

Clinostigma ponapensis

Clinostigma ponapensis palm is a dominant canopy tree in Pohnpei's upland forest. It had a significantly wider presence among quadrats and was more abundant at time 0 in MPF than in SAF (Chapter 6, also Table 8.1). *Clinostigma* recruited in significantly greater numbers in GPF but that may be due in part or wholly to a clumped distribution between MPF and GPF at time 0. However, as I found for *Campnosperma*, new recruitment among MPF and GPF quadrats correlated positively with light, indicating that *Clinostigma* establishes more in the higher light areas within the forest. Among all plot types, no correlations with light were found, probably because *Clinostigma* was recruited only under a few remnant adults in SAF rather than across a range of light conditions.

Clinostigma uses several mechanisms to establish, including copious fruiting. It was the second most widely distributed (number of seed-traps hit) seed-rain species in both MPF and SAF and was fifth in abundance in both MPF and SAF (Winthrop 1998), although in SAF seeds came from only a few plants due to its overall low stocking of woody stems. It was also a prominent member of the forest advance-growth population but the seedlings did not endure the shade-suppression for as long as

the other dominant, *Parinari* (see section 8.4.3). Seeds of *Clinostigma* were relatively abundant in the MPF seed bank (13 % of all seeds), but this was probably an artefact of copious seeding rather than persistence; the relatively large and thin-coated seeds were in all probability unviable (Gardner 1997). Therefore, *Clinostigma*'s strategy for establishment is through seed rain and an advance growth population of small, moderately shade-tolerant seedlings. Abundant seed rain replenishes the advance-growth population as well as recruiting directly if coinciding with small-scale forest disturbance.

Seedling growth of *Clinostigma* was highest in GPF and lowest in MPF, but sample sizes were too small to gauge very effectively its growth habit. A larger demographic study of *Clinostigma* would be worthwhile, particularly to gain a clearer picture of its growth habit. The results do suggest, though, that *Clinostigma* juveniles grow best in the medium light conditions typically associated with small-scale forest disturbances and under canopies dominated by conspecific adults. Canham et al. (1994) showed that the successional status of a species is related to the shade cast by its adult trees. Hence, with its tall, thin trunk, no branches, and only a small frond mass at the top of the palm, *Clinostigma* casts a narrow and variable shade. Large sunflecks are probably a higher component of the forest light environment under *Clinostigma* than more densely crowned species, although I did not examine this. Lateral light may also be high where *Clinostigma* adults are predominant, depending upon the slope and aspect of the site. Seed rain and recruitment of *Clinostigma* were plentiful under conspecific adults, which partly explains the new-recruitment correlation with light among forest quadrats.

Juvenile recruitment, growth and survival patterns, plus adult canopy architecture all suggest that *Clinostigma* is less late-successional than species like *Parinari*, and regenerates best in moderate light conditions typical of small gaps and partially shaded zones of larger gaps such as gap-forest edges. This regeneration strategy is similar to *Prestoea montana*, a dominant canopy palm in Puerto Rican mid-altitude forest (Devoe 1990).

Campnosperma brevipetiolata

Campnosperma brevipetiolata is a common large-canopy tree on Pohnpei and is found throughout Micronesia and Solomon Islands (Burslem & Whitmore 1996). Its contrasting size-class distributions in forest vs. SAF (see Table 8.1) indicate that

Campnosperma regenerates successfully in higher light areas typically found only after large-scale disturbance. Conversely, it does not regenerate well in the low-moderate light of most forest areas.

Campnosperma was the most common forest-seed-bank species, contributing 35 % of all seeds in the closed-forest seed bank (Gardner 1997). The seeds are small with a hard endocarp, traits commonly associated with persistent seed bank regenerators (ibid.). In contrast, only 4 % of seeds in the SAF seed bank were *Campnosperma*; most likely, many of the seeds had already germinated (ibid.). *Campnosperma* was also the most widely dispersed species in the Pohnpeian mature-forest seed rain and dispersed the third greatest number of seeds (Winthrop 1998).

Deep litter and low light do not inhibit *Campnosperma* germination. Recruitment of *Campnosperma* was common in MPF and GPF (Table 8.1), despite only low-moderate light levels and generally deep litter cover, particularly during and following the drought. Also, my study had no upturned root plates to expose the soil. Nevertheless, in the forest quadrats, total new recruitment of *Campnosperma* per quadrat correlated positively with light. High light and low litter volumes usually enhance germination of early-successional species (Kennedy & Swaine 1992; Molofsky & Augspurger 1992).

By 15 months, GPF and SAF both contained significantly more *Campnosperma* than MPF. Few survived in GPF (or MPF). In the forest, no *Campnosperma* seedlings survived for 15 months and no individuals recorded heights between 0.2 m and 18 m. Given the small size of Pohnpeian gaps in the absence of typhoons plus the high residual vegetation of advance-growth seedlings and saplings, the chances of a *Campnosperma* reaching canopy height in a small gap is remote. Similarly, Sheely (1995) studied *Campnosperma*'s demography on Pohnpei and found that recruitment, survival and growth of juveniles taller than 20 cm was low in mature forest plots that had experienced little human or natural disturbance. Conversely, open, disturbed plots had high juvenile recruitment and their survival and growth was significantly greater than in the shaded forest plots (ibid.). Comparisons among my plot types for seedling or sapling growth of *Campnosperma* were impossible because almost no seedlings survived from one census to the next in either MPF or GPF, but Sheely (1995) found that seedlings showed high phenotypic plasticity.

In summary, *Campnosperma* dominates the seed rain and soil seed bank in MPF, is present as a canopy tree in MPF but not as saplings, has greater survival and

growth in SAF, and is spatially clustered in open forest areas. Although it can recruit in low-moderate light levels common in MPF and GPF, only in large gaps can *Campnosperma* survive and grow through the juvenile stages. These characteristics strongly suggest that the species regenerates, and probably dominates initially, after large-scale disturbances such as typhoons, as it does in the Solomon Islands (Whitmore 1974).

8.6 Conclusions

In this thesis, I built a picture of forest regeneration in Pohnpei's uplands to examine the role that advance growth plays in regeneration following small-scale tree-fall gaps (MPF-GPF) and larger, human-induced forest disturbance (sakau-agro-forest). The picture, however, is determined to an extent by the scale at which I viewed the forest. Comparisons across different scales were an underlying theme in this thesis: measurement scales (plot types vs. plots vs. quadrats); life-history stages (seedlings vs. saplings); experimental disturbance and light ranges (MPF and GPF alone vs. all three plot types together); early- and late-successional species vs. individual species characteristics within those groups; and natural forest disturbance scales.

The disturbance survey and discussion illustrated that frequently shed palm fronds and branch-falls, through to single- and few-tree falls like GPF gaps operate both spatially and temporally on a small scale on Pohnpei (sections 8.1, 8.3.1). Overlying and interacting with this scale are rare, but highly destructive, typhoons that disturb large areas and have long return cycles. Both scales are equally important because although typhoons produce large gaps, the species composition and structure on site before the typhoon as well as vegetation composition surrounding the site influences what grows afterwards. This has serious implications for forest regeneration after the next typhoon, given the continued degradation of forest areas to cultivate sakau (see next chapter). Forest conversion to sakau cultivation produces large, highly modified gaps; these disturbances have been frequent over the past two decades. This activity defies the natural forest-disturbance regime, where larger disturbances are much rarer than smaller ones.

Among field measurements, within-plot type variation was greatest in SAF because it included remnant patches of forest through to very open grassy areas. GPF was the next most variable: felling trees had the effect of expanding the range of micro-environmental conditions without necessarily shifting the mean significantly. Plot means and plot type totals (stem frequencies) highlighted the broad successional and light gradients operating over a wide environmental range. At the all-plot-types and plot-mean levels, early- vs. late-successional species-groups and large gap vs. small gap dichotomies were generally clear. Yet, when I excluded from analyses the long light range provided by SAF data, relationships amongst plant and micro-environmental variables were often weak or non-existent. Relationships were usually clearest in plot/plot-type-level analyses inclusive of all plot types; conversely, relationships were weakest in quadrat-level analyses covering only mature- and small-gap-phase forest data. Two main reasons can explain this. Firstly, the experimental design, the resolution and accuracy of measurements, the short time period for measurements, and the co-linearity among some variables affected my view of forest processes. Plot means were centred upon averages of data from many plants (among all woody species, 100-500 plants per plot). As such, they hid much variability of interest, but this "statistical noise" reduction sharpened the broad contrasts among plot types and species successional groups. In contrast, the highly variable quadrat-level data arguably better represented individual plant realities, particularly for seedlings, but, like Turner (1990b), my measurements were insufficiently detailed to resolve such small-scale spatial and temporal complexity. For example, factors such as litter and debris were either uncorrelated with plant variables, or they may have contributed in some circumstances but these circumstances could seldom be determined from my measurements.

Secondly, at a small scale in the forests, light and other environmental variables may be less important in driving regeneration processes than biotic interactions and stochastic factors (Turner 1990b). My results and those of others (e.g., Ferguson & Adams 1980; Uhl et al. 1988; Brown & Whitmore 1992; McClure et al. 2000) have shown the strong influence of pre-gap factors such as plant size, age, and pre-gap vigour in determining post-gap plant growth and survival of advance growth. Hence, pre-gap processes are arguably as important as gap processes (Brokaw & Scheiner 1989). Furthermore, as seedlings and saplings will rarely reach adulthood in the few years that light is enhanced in a small gap, the return cycle and duration of the gap

phase will strongly influence an individual plant's long-term success (Canham 1989). This is why advance growth dominates the regeneration in the small gaps of GPF.

Like the plot means, seed groups were centred upon the mean responses of species within a certain seed-mass range, but each group hid much variation of interest. Seed groups show the broad-scale picture of the forest across small and large gaps. Within each seed group is a more detailed, more varied picture than early- vs. late-successional, but I only had sufficient data on a few species to gauge the more complex picture of species behaviour.

Advance growth clearly plays a dominant role in small-scale forest dynamics on Pohnpei. Disturbances ranging from *Clinostigma* fronds and branch-falls through to single- or few-tree falls produce only subtle micro-environmental changes. Altered light levels and an increased heterogeneity in litter are important to individual plants at a local scale, but are not the sharp contrasts between gaps and mature forest that are generalised in gap-phase theory. Light is rarely elevated enough from these disturbances (or) for long enough to offer species which require high light for survival, typically those with lighter seed masses, the opportunity to survive and utilise their faster growth rates. Also, litter and woody debris cover may be more spatially heterogeneous in the gap phase, but even in an uprooted-tree gap, few areas lose litter sufficiently to promote mass germination of small-seeded species, such as those from the soil seed bank. Tree and shrub species that are better adapted for survival in the low-moderate light conditions most frequently encountered in mature- and gap-phase forest, typically those with relatively large seed masses, establish from advance growth and/or seed rain.

The prevalence of advance growth in Pohnpei's upland forest means that regeneration in the small-scale single tree falls of GPF is via cyclic replacement (*sensu* Whitmore 1998, p.27). That is, in small disturbances, late-successional species, that dominated mature-phase forest (MPF), were self-perpetuating into the gap phase. New recruitment in GPF gaps mirrored the species present on site already, which were predominantly later-successional tree species. The only species recruited in disproportionately larger numbers was the early-successional *Campnosperma*, but its abundant small seedlings almost never survived from one census to the next. Thus, in the absence of a typhoon, small-scale gap-phase regeneration may alter the competitive hierarchy among individuals on a site (e.g., at the quadrat-level), but over a plot-scale, the common species will change little. This is in-line with the classic forest mosaic

theory and its observations of patch-level vs. larger-scale dynamics (Aubreville 1938; Richards 1952).

It was not possible to study regeneration following a large-scale natural forest disturbance such as a typhoon. Nevertheless, from comparisons of the seed rain (Winthrop 1998), seed bank (Gardner 1997), and advance growth (present study), I predict that large-scale forest regeneration would occur predominantly as secondary succession via "initial floristics" (sensu Egler 1954). That is, most species - early and late successional - are present on site at the time of disturbance or soon afterwards, but faster growth rates in high light conditions mean that early-successional species would dominate the site initially (Whitmore 1983). Elevated light levels and exposed soil on upturned root plates would promote regeneration of *Campnosperma* and other native early-successionals such as *Macaranga* which are present in the mature-forest seed bank or the seed rain. Physical damage and photosynthetic shock would likely kill many advance-growth seedlings and saplings, in much the same way as seedling mortality was greater in GPF plots during the drought. Advance-growth seedlings might be overtopped within a few months by faster growing earlier-successional species. Nevertheless, as always, some advance growth would persist and continue to grow under early-successional tree shade. Eventually, mid and late successional species would grow up, over-top and shade out the early successionals, as forest stratification described in Oliver and Larson (1996).

In contrast to small- or large-scale natural forest regeneration, the size of sakau plots studied, though within the potential size for typhoon-level multiple-tree falls, combine with cultivation processes to create markedly different regeneration processes (Allum 1996). Consequently, sakau agro-forest was mostly regenerating by secondary succession via "relay floristics" (Egler 1954). In most areas of SAF, later-successional species were not present on site because advance growth was destroyed by weeding and gap formation, and seed rain to SAF was deficient in larger-seeded species (Winthrop 1998). Hence, there will be a successive appearance and eventual disappearance of groups of species in the plots (Egler 1954, p.414).

Signs of successional change over 15 months in SAF included: an unmeasured but likely decrease in canopy openness; increased litter depth; rapid tree growth; and reduced grass cover. In addition, a few individuals of later-successional species were able to persist as remnant adult trees, or establish under the remnant adults or along gap edges, thus representing a small component of initial floristics. Other more mid-

successionals like *Aglaia* and *Pandanus* have been able to re-establish in the edge or remnant zones in small numbers throughout cultivation but particularly after abandonment. Nevertheless, the dominance of non-woody species is delaying the rate of successional change.

Left alone, abandoned SAF plots will eventually become secondary forests and, perhaps in 40 years, vegetation could attain a canopy height similar to mature-phase forests. However, regeneration speed and success will depend upon a number of factors, including SAF plot size and length of cultivation, and it may be a long time before species composition in the abandoned SAF plots resembles that of mature-phase forest. This will be discussed in the final chapter.

Chapter Nine: The Future for Pohnpei's Forests

Unfortunately for Pohnpei's upland forests, the hypotheses underpinning this thesis have been proved true. Regeneration in small, abandoned sakau plots mostly follows a process of secondary "relay floristics" succession. In contrast, small patches of forest, that is, excluding rare but severe and widely-spread, typhoon-induced disturbance, regenerate via the gap phase by cyclic replacement rather than succession; large typhoon disturbances regenerate predominantly by "initial floristics". The population of regenerating seedlings and saplings in gap-phase forest mirrors the species composition of the adults in mature forest. Advance growth and seed rain, which are the main mechanisms used for reestablishment by mid-late-successional/larger-seeded tree species (Table 8.2), are failing after forest clearance and clean weeding of tree seedlings. The important implications of this for future forest composition, and the challenges posed and potentials held for successful forest recovery on Pohnpei are discussed in this chapter.

Regeneration of mid-late successional species in abandoned sakau plots is challenged most in seed supply and germination through to seedling establishment rather than in the survival and growth of established large seedlings and saplings. Seedling and sapling health within species was higher in SAF and growth rates for those with heavier seed-mass (seed groups 1 and 2) were similar to or greater than in GPF. This means that where forest tree and shrub species can establish themselves in SAF, the higher light helps them grow quickly and thereby assists their future chances of survival; I found that survival was clearly related to plant size.

Seedling establishment of late-successional species in SAF is handicapped at three critical stages. The first of these is inadequate seed supply. Species must physically arrive in order to have any chance of establishment. Winthrop (1998) found almost distinct seed rain populations, with *Parinari*, *Myristica*, *Syzygium*, and other late-successionals absent from SAF seed-rain. Also, Gardner (1997) showed that the soil seed bank holds no large-seeded species, with the possible exception of *Clinostigma* (but see comments, p.191). This is highlighted in Table 8.2, where common species in the heaviest two seed-mass groups were found not to use the seed-bank mechanism, whilst species with lighter seeds used the seed bank and never

advance growth. Seed supply is more likely along the SAF / forest edges and under remnant saplings and adults within the sakau plots. Seed availability for forest tree species, especially for large-seeded species, is a major limiting factor to forest restoration elsewhere (Hardwick et al. 1997; Holl et al. 2000; Wijdeven & Kuzee 2000).

Secondly, for the few large seeds that fall in open SAF areas, their chances of seedling recruitment may be hindered by very high light and especially by lower relative humidity, particularly during droughts (Hardwick et al. 1997; Holl et al. 2000). In addition, seed predation can be greater in large open areas than in forest (Holl et al. 2000; Wijdeven & Kuzee 2000), but seed predation rates are not known for Pohnpei.

Thirdly, even if large seeds do germinate, the strong positive correlation I found between light and coverage of ferns and grasses means that there will be fierce competition for resources. In abandoned tropical pasture lands, Holl et al. (2000) found that seed supply and seedling competition with grasses were the two greatest impediments to forest recovery. Within the more shaded edges and remnant zones of SAF, however, where seed supply is likely to be higher, micro-environmental conditions are better for seed germination and competition from non-woody cover will be less intense. Also, seedling growth can be greater in partial shade than full sun because plants are not photosynthetically stressed, plus they may receive more nutrients from a greater litterfall (Loik & Holl 1999). Clearly, efforts to restore late-successional species are best directed to speeding seedling establishment in these edge and remnant zones.

Early-successional woody species have better dispersal to sakau plots than late-successsionals due to their smaller seed size, greater seed production and, depending upon the length of cultivation and plot size, presence in the seed bank. These trees and shrubs grow rapidly in the high light conditions in SAF; however, early establishment can be thwarted by strongly competing non-woody species.

9.1 Factors affecting future upland-forest composition

9.1.1 The impacts of continued forest clearance for sakau cultivation

One of the biggest factors affecting the integrity of upland forest is the rate of forest conversion and its impacts on propagule supply. As more upland forest is

cleared, the potential source of seeds from adult fruiting trees diminishes and the habitat for seed-dispersing birds and bats is reduced. If the present rate of forest clearance is maintained, the matrix of forest with sakau-agro-forest will expand more towards the latter condition. Young et al. (1987) found that the seed rain in forests changes in relation to the composition of surrounding vegetation. Thus, if Pohnpei's upland forest continues to be fragmented through forest clearance and sakau cultivation, the seed rain in forest surrounded by cultivated clearings will be increasingly composed of early-successional and weedy species. Likewise, abandoned SAF plots will be ever more likely to become dominated by weedy species. Moreover, the high turnover within the advance-growth seedling populations means that a continual and plentiful supply of late-successional seeds is crucial to the integrity of advance-growth populations in forest areas. Hence, as fragmentation increases, restoration of degraded areas becomes harder and the continued viability of forest fragments is jeopardised.

Also, if seed banks in the uplands become increasingly filled with long-lived weedy species, what will happen in the next big typhoon? Normally, Pohnpei's native early successional trees like *Campnosperma* and *Macaranga* germinate en mass from the soil seed bank and dominate the early forest regeneration. Gardner (1997) found these two species were very common in seed banks under mature forest but were rare in seed banks under sakau plots, where grasses dominated. The increasing fragmentation of the upland forest and altered seed patterns may therefore seriously affect the uplands during the next large typhoon.

9.1.2 The impacts of a continued decline in bird populations

The health of forest bird populations will have a major impact on forest recovery, especially large-gaped birds such as *mwuroi*/Micronesian pigeon (*Ducula oceanica*). Buden (2000) found most Pohnpeian forest bird populations have declined dramatically since (at least) the 1980's, which he attributed to habitat loss from upland-forest clearance as well as hunting. If the *mwuroi* numbers continue to decline, seed dispersal away from parent trees of *Clinostigma*, *Myristica* and other large-seeded species will be increasingly less likely. Tree distributions will become even more clumped than they are already. This will reduce further the chances of these species reaching recovering sakau plots. Successful regeneration of such areas will rely more heavily on human intervention for seed dispersal.

Guns have increased the threat to and death of native forest bird species such as *mwuroi*. Traditional weapons required more skill and effort and meant that fewer birds could be killed at one time (Buden 2000). Guns are now combined with the loosening of social and ecological connections between people and their physical environments so that people can kill more, appreciate the value of what they are killing less, and are less aware of the consequences. Killing *mwuroi* was/is a Pohnpeian custom and yet when that was truly meaningful was at a time when there were no guns, no imported canned meats, and people lived, by necessity, in closer connection with their physical environments. Hunting is probably of considerably less importance in declining bird numbers than forest clearance. Nevertheless, it will not help.

9.1.3 The impacts of global warming, drought and fire

The El-Niño drought of 1997/1998 caused considerable mortality in the forest I studied. Global warming may increase the frequency, intensity and duration of droughts that will disadvantage species with small seedlings as advance growth the most, for example, *Clinostigma*, *Syzygium*, and *Aglaia*. Although *Campnosperma* mortality was the highest and I observed numerous adult tree deaths, the probability of *Campnosperma* recruiting is higher than other forest species because of its presence in the seed bank and wider distribution of seed rain. Species like *Clinostigma*, however, and the less common late-successionals, will have more difficulty re-establishing.

Parinari is the least affected by drought in the advance growth because of its larger seedling size, but fire is indiscriminant and devastating for all mid- and late-successionals that rely on the advance growth mechanism. Through its destruction of advance growth, forest fires greatly retard regeneration processes. Also, higher light and substantially reduced litter in burnt forest areas are avenues for establishment of early and mid-successional trees rather than later-successional tree species, as well as weedy ferns, grasses and vines, (results, p.137-138, Woods 1989).

Future El Niño droughts are likely to provide more opportunities for the forest to burn. When I asked people why Pohnpeians (mostly males) lit fires in the drought, the common responses were "because we can" (that is, normally it is too wet for the vegetation to burn well), and "because it's fun". These sentiments were similar to those expressed in Papua New Guinea (Caufield 1991, p.265-266), although there they also burn more to create gardens. Unless Pohnpeian males' excitement of starting forest fires kerbs, further forest fragmentation and retarded forest recovery is likely in

future droughts. Global warming might also alter the frequency and intensity of tropical cyclones, but presently climate change models can not confidently predict what might happen (Hulme & Viner 1998).

9.1.4 Social impacts

The future of Pohnpei's forests will depend considerably upon the perceptions and priorities of Pohnpeian society, especially young people since they hold the future. The close interrelationship of older Pohnpeians with their physical environment needs to be passed on to younger generations in a uniquely Pohnpeian way. For example, a wealth of ethno-botanical knowledge exists among older Pohnpeians, but fewer young people are interested in that knowledge now and in the lifestyle that it entails. The present school education system is based on the western style of learning, including all the dominant western perceptions of people and their surroundings that are embedded in that thinking. The formal education system must incorporate more of an understanding of the world through Pohnpeian eyes.

Ultimately, Pohnpeians young and old need to remember and appreciate anew the relevance and importance of maintaining a healthy upland forest. Pohnpeians need their forests not only for the human utilitarian reasons – water quality, land stability, forest products, etc. – but to maintain their unique identity, that ecological and social fabric inherent in the Pohnpeian way of life.

It is with the above seedling-establishment difficulties and factors affecting future forest composition in mind that I conclude, firstly, with suggestions to mitigate the detrimental impacts of continued cropping, and secondly, with suggestions to assist recovery of formerly cultivated sites.

9.2 Mitigation of sakau cultivation impacts: small plots, seed trees and advance growth seedlings and saplings

Obviously it is preferable to have no more forest clearance for sakau cultivation in the uplands, particularly in the area demarcated as a watershed forest reserve. Whilst forest conversion continues, however, I suggest that farmers cut small plots, leaving as many adult trees of late-successional species as is practical. Late-

successional seed trees are critical for successful regeneration because their seed dispersal capabilities are quite low and they usually lack soil seed banks. Not only do remnant adult trees supply seeds but their shade can reduce photosynthetic stress and therefore enhance tree seedling growth compared with seedlings in very open sites (Loik & Holl 1999). The shading effect of remnant adults will be especially important in the large sakau plots because of their greater areas of full sun-exposure compared to smaller plots, where much of a plot may receive partial shade from surrounding vegetation. In addition or as an alternative, farmers could cut small plots but within the plots retain some seedlings and/or saplings of advance growth, the larger the better since greater size improves survival.

Retaining mid and late-successional juveniles while cultivating sakau plots helps to ensure that the benefits people gain from these species are continued. For example, strong, straight and rot-resistant *Parinari* poles are traditional housing materials (Merlin et al. 1992). Likewise, the bark of *Cinnamomum carolinense* Koidz. makes a desirable tea, *Garcinia*'s wood makes very hot-burning firewood, and *Clinostigma* saplings are cut for the sweet pith inside and the fronds are used for temporary shelters (ibid.).

It is tempting to suggest that sakau growers should cultivate their (small) plots only for short periods of time before moving in order to increase the seed bank levels and hence provide a greater supply of early to mid successionals for re-colonisation. Certainly, small plots are strongly recommended. Allum (1996) found that regeneration is slowed the longer a sakau plot is cultivated and the greater it is in size. And yet, regeneration success also depends on the composition of contiguous vegetation (Young et al. 1987). Short rotation ages of plots coupled with large numbers of sakau growers comes at a price: if people move on more quickly while the soil is still good for sakau as some people do now because of sakau theft, the area of cleared forest will increase (see section 9.1.1). Allum (1996) showed that plots under shorter crop rotations had greater numbers of trees and shrubs, but if forest clearance is not abated very soon, there will be fewer woody species propagules, especially larger-seeded ones, available for either condition.

9.3 Forest restoration strategies

Grasses, vines, and especially ferns dominated much of the sakau agro-forest areas that I studied; grasses were more common in the most open areas. Over the 15 months of the study, tall ferns began to smother grasses and I recorded their decline. In time, the ferns will be shaded out by fast-growing, early successional trees and shrubs; this has already begun in some areas. The shade cast by early-successional trees suppresses non-woody cover, but provides suitable conditions under which mid- and late-successional species can germinate, assuming, of course, that the seeds arrive in the first place. These species will eventually take over as the shorter-lived, early-successional trees die.

To assist regeneration of these degraded forest areas, we need to accelerate and overlap the successional phases, particularly the period of early dominance by ferns and grasses, but with the minimum of human intervention. To do this, I suggest, first, manually cut down grasses and ferns[19], then directly seed or transplant seedlings (wild or nursery-grown) of fast-growing early to mid-successional tree and shrub species in to the open zones of the sakau plots (9.3.1). Secondly, transfer seeds (or seedlings) of mid to late-successional species in to the edge and remnant zones (see 9.3.2). Seeding and/or planting should not be done in drought conditions.

9.3.1 Direct seeding of early-mid-successional trees such as *Campnosperma* and *Macaranga* to SAF open sites

Given their importance in natural, large-scale forest disturbance, *Campnosperma* and *Macaranga* would be my first choice for species to consider directly seeding or planting in open SAF areas. Other early to mid-successionals should be chosen with the intention of quickly offering an attractive source of food or perching site for birds. Species such as *Ficus tinctoria* are valuable because they can grow quickly to reproductive age and their fruits are very attractive to many birds. The

[19] Chemical herbicides are not recommended, even though they are probably faster and more efficient at clearing vegetation than manual clearing. Chemical weed control is relatively expensive for Pohnpeians, has seldom been used to date on the island, and would require purchasing safety equipment, which is also expensive. Furthermore, the long-term human and ecological safety of herbicides has not been proven (see, e.g., Steingraber 1998) and the upland forests are watershed reserves for most of the people on the island. Traditional Micronesian agroforestry controlled the size and timing of forest gaps to promote the growth of a farmer's desired species (Raynor 1989; Falanruw 1998) rather than clearing large areas and then needing large-scale ways to kill the inevitable sun-loving grasses and ferns.

provision of fruits and perching sites for birds is vitally important in forest restoration: when birds come to feed or perch in a regenerating site they bring in more seeds from outside the plot and thereby help to accelerate forest succession (McClanahan & Wolfe 1993). Other species could include *Melastoma*, *Maesa carolinensis* Mez, and *Claoxylon*.

In plots that have been cultivated for only a short time, for example, my SAF plots, which were cultivated for 3-11 years (c.f. 20-30 years for Allum's (1996) old sakau plots), some seeds of early successionals like *Campnosperma* and *Macaranga* may be available in the seed bank. The usefulness of the seed bank will depend upon the plot size and history. The longer a sakau plot is cultivated, the fewer seeds are in the seed bank and Gardner (1997) showed these were predominantly grasses and weedy tree species like *Morinda*. Therefore, in the small, less-cultivated plots, natural regeneration from the seed bank and seed rain from the forest closely nearby will supplement direct seeding and/or planting.

9.3.1 Transplant large seeds to edges

At the nearest fruiting time to when they abandon their plots, I suggest farmers collect seeds of *Parinari* and/or *Myristica* and *Clinostigma* from where adult trees are fruiting abundantly in neighbouring forest. Obviously, this needs to be done without impairing the seed supply to the intact forest; however, *Parinari* and *Clinostigma* both fruit quite copiously and it is easy to find and collect seeds from the forest floor. Scatter the seeds in SAF where woody cover provides some shade and grass and fern cover has been suppressed, for example, under tall saplings of early-successional trees or remnant late-successional adults. In the absence of multiple clearing of non-woody cover, dispersal of late-successional seeds to the higher light, central areas of sakau plots should best be done once early-successional trees have established so they can partially shade the later-successional seedlings and, most importantly, restrict non-woody cover. Any seeds of other mid- or late-successional species that the person finds in large quantities in neighbouring forests could be transferred to the edge zones. Mid-successional species like *Aglaia*, *Pittosporum*, *Glochidion marianum*, or *Claoxylon* are capable of tolerating moderately high light conditions provided fern and grass cover is low.

Pohnpei has a number of social and ecological advantages for successful forest restoration:

- Its tropical wet climate allows fast growth in high light areas (i.e., not necessarily in closed forest). For example, some early successional trees in SAF grew up to three metres in one year.
- Introduced browsing animals presently cause few problems in the forest. Control or eradication of introduced herbivores in forest restoration areas requires a major effort in Pacific islands like Hawaii and New Zealand. Small Philippine deer, jungle fowl and pigs are present in Pohnpei's forest but their populations are sufficiently low to make browsing impacts almost negligible. Nevertheless, deer browsing causes considerable damage on Guam and may have caused significant damage in Pohnpei's forests in the past when the deer population was higher (Wiles et al. 1999). Pohnpei needs to ensure that domesticated animals are well controlled, particularly goats, which have caused many problems in Hawaii's forests. Although there are only a few on the island, it would be preferable to limit further introduction of goats.
- Pohnpei has an effective group of native pioneer tree species, including *Cyathea*, *Campnosperma*, *Maesa*, and the endemic *Macaranga* to assist early restoration of degraded forest sites.
- Fire is not commonly used for forest clearance for agriculture. Fire sets back succession considerably (e.g., Woods 1989).
- Much of the uplands is still at least partly forested.
- Pohnpei still has a large subsistence base in the lowlands where people live. This at least reduces the scale of need for cash-earning activities like sakau crops.
- Pohnpei has traditionally had a very strong cultural identity. For example, Pohnpei was the only state in the Federated States of Micronesia to reject the US-FSM compact proposal during compact negotiations because many Pohnpeians thought it infringed upon their autonomy and culture (Ashby 1993). This strength can help Pohnpeians to better appreciate and protect their cultural and ecological identity in the face of strong and increasing western influence.
- Pohnpei has an increasingly strong and effective grass-roots network of people and groups involved in social and ecological conservation.

In summary, if the social intention is strong to restore degraded upland forest areas, then some form of manual fern and grass cutting followed by seeding or planting of early to mid-successional trees and shrubs in SAF open zones and mid to late-successional tree species in the edge and remnant zones, is suggested. Species that can attract birds will be especially valuable. These restoration suggestions are simple for two reasons. Firstly, I am aware that few financial or institutional resources are presently available to carry out any grandly detailed replanting scheme I might offer. Secondly, I simply don't know enough about the reproductive ecology of species like *Campnosperma* and *Macaranga*, or the practical capabilities and facilities on Pohnpei to make such detailed suggestions. For example, *Campnosperma brevipetiolata* was grown as a native plantation species in Solomon Islands, but was later discontinued because along with poor growth form, there were seed collection and handling difficulties (Chaplin 1993).

Further research is needed to find financially and practically viable mass-seed collection for direct sowing or a planting programme. The success of direct seeding will depend, among many things, upon the germination rate of the seeds collected, how well the seeds store, what seed treatments are needed (e.g., scarification), the extent of seed predation once sown, and weather (i.e., no droughts). Direct seeding needs to be compared with transplanting nursery (or wild) seedlings to determine which method is more effective. If seedlings are grown in a nursery, for example at the forestry station at Pohnlangas, overall effectiveness will depend upon nursery and planting practices as well as transportation ability to the sakau plots.

A growing body of scientific literature and practical experience is exploring forest restoration issues such as these. It is the job of a future researcher to examine the literature and formulate and test restoration procedures that are most appropriate for Pohnpei. Regeneration success can later be evaluated by, for example, sampling the composition and frequency of new recruitment under restoration plantings compared with non-planted sites.

Restoration strategies are but one part of an overall goal of ecological and social sustainability. It is not enough to restore forest cover if by doing so we reinforce a perception of our physical environments that is driving the deforestation. Recent colonial Pacific history and current economic globalisation have rapidly immersed Pohnpei in western (particularly US) culture, including a western perception of our

physical and spiritual worlds where humans are separate from the rest of nature. Ecological breakdown in the upland forests mirrors a social breakdown as Pohnpeians relate less intimately with their human and non-human fellows. In this thesis, I tried to be aware of the social and historical issues creating the deforestation and then offer ecological-research-based restoration suggestions appropriate to the goals of the overall Pohnpeian community-based-and-strengthening environmental programme.

Pohnpei is not alone in its challenges. In a sense, the island is a microcosm of what is happening to varying degrees throughout the Pacific and much of the rest of the world. Pohnpeians will continue to interact with people living outside the island, particularly those from western countries that are most influential in Micronesia: USA, and to a lesser extent, Japan, Australia, and perhaps New Zealand. Given the continued western influence, some of the greatest assistance *menwai* (foreigners) can offer Pohnpei is to try to heal the social and ecological challenges in our own countries.

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Appendices

Appendix A: A list of all species recorded

Species	Family	Pohnpeian name if known, + ID notes [ ]
Aglaia ponapensis Kaneh.[20]	Meliaceae	marasau
Alocasia macrorrhiza (L.) G.Don	Araceae	oht
Alpinia carolinensis Koidz.	Zingiberaceae	iuiu
Antrophyum callifolium Blume [=Asplenium 1]	Polypodiaceae	
Asplenium nidus L. sensu lato [=Asplenium 2]	Polypodiaceae	Tehnlik
Asplenium polyodon G.Forst. [=Asplenium 3]	Polypodiaceae	
Asplenium sp.	Polypodiaceae	peipei eni
Barringtonia racemosa (L.) Spreng.	Lecythidaceae	wih
Blechnum orientale L.	Polypodiaceae	marek en leng
Blechnum sp.	Polypodiaceae	
Bulbophyllum sp.	Orchidaceae	
Campnosperma brevipetiolata Volkens	Anacardiaceae	dohng
Cananga odorata (Lam.) Hook.f. & Thomson	Annonaceae	seir en wai
Canthium barbatum (G.Forst.) Seem.	Rubiaceae	Kenmant [smooth one]
Cinnamomum carolinense Koidz.	Lauraceae	madeu
Claoxylon carolinianum Pax & Hoffman	Rubiaceae	kehi
Clinostigma ponapensis (Becc.) Moore & Fosberg	Arecaceae (Palmae)	kotop
Cyathea nigricans Mett.	Cyatheaceae	katar
Davallia solida (G.Forst.) Sw.	Polypodiaceae	uhuhl en kieil
Dendrobium sp.	Orchidaceae	keleken
Derris elliptica (Roxb.) Benth.	Fabaceae	peinuhp
Diplazium sp.	Polypodiaceae	
Discocalyx ponapensis Mez	Myrsinaceae	
Elaeocarpus carolinensis Koidz.	Elaeocarpaceae	sadak
Embelia palauensis Mez	Myrsinaceae	
Eragrostis sp.	Poaceae (Graminae)	reh maikol
Fagraea berteria var. *sair* (Gilg & Benedict) Fosberg	Gentianaceae	pwuh (en pohnpei)
Ficus tinctoria G.Forst.	Moraceae	nihn
Flacourtia rukum var. *micronesica* Fosberg & Sachet	Flacourtiaceae	[kenmant family]
Flagellaria indica L.	Flagellariaceae	idanwel
Freycinetia ponapensis Martelli	Pandanaceae	rahrah
Garcinia ponapensis Lauterb.	Clusiaceae	kehnpuil
Glochidion marianum Mull.Arg. [=Glochidion]	Euphorbiaceae	luwikidenlol
Glochidion ramiflorum G.Forst. [=Glochidion 2]	Euphorbiaceae	mwehk
Gynotroches axillaris Blume	Rhizophoraceae	
Hibiscus tiliaceus L.	Malvaceae	keleu
Hoya schneii Schltr.	Asclepiadaceae	
Humata banksii Alston	Polypodiaceae	
Hypolytrum sp.	Cyperaceae	[pwoaki lookalike]
Ipomaea sp.	Convolvulaceae	oomp
Ixora caseii Hance	Rubiaceae	ketieu
Lemmaphyllum accedens (Blume) Donk	Polypodiaceae	
Lindsaea lobata Poir. [=Lindsaea 1]	Polypodiaceae	
Lindsaea repens var. *lingulata* Kramer [=Lindsaea 2]	Polypodiaceae	
Lycopodium phlegmaria var. *longifolium* Spring	Lycopodiaceae	
Macaranga carolinensis var. *grandiflora* Pax & Hoffman	Euphorbiaceae	apwid
Maesa carolinensis Mez	Myrsinaceae	kehsile

[20] Pannell (1992) suggested that *Aglaia ponapensis* may fall within *A.mariannensis* Merrill, but because the revision was only tentative and requiring further study, I retained A. *ponapensis*.

Species	Family	Pohnpeian name if known, + ID notes [ ]
Mapania pandanophylla (F.Muell.) K.Schum	Cyperaceae	pohkee
Marrattia sp.	Marrattiaceae	
Melastoma malabathricum var. *marianum* (Naudin) Fosberg	Melastomaceae	p/kisetikimei
Merremia peltata (L.) Merrill	Convolvulaceae	iohl
Microlepia speluncae (L.) T.Moore	Polypodiaceae	
Morinda citrifolia L. var *citrifolia*	Rubiaceae	weipwil
Myristica insularis Kaneh.	Myristacaceae	karara
Nephrolepis biserrata (Sw.) Schott	Polypodiaceae	rehdil
Pachygone ledermanii Diels	Menispermaceae	
Palaquium karrak Kaneh.	Sapotaceae	kalak
Pandanus cominsii var. *micronesicus* B.C.Stone	Pandanaceae	mwatal
Parinari laurina Gray	Chrysobalanaceae	ais
Paspalum conjugatum Bergius [=Paspalum 1]	Poaceae (Graminae)	reh
Paspalum orbiculare G.Forst. [=Paspalum 2]	Poaceae (Graminae)	reh nta
Peperomia sp.	Piperaceae	
Piper methysticum G.Forst. [=Piper 2]	Piperaceae	sakau
Piper ponapense C.DC. [= Piper]	Piperaceae	konok
Pittosporum ferrugineum W.T.Aiton	Pittosporaceae	kamal
Premna obtusifolia R.Br.	Verbenaceae	teewek
Procris pendunculata (G.Forst.) Wedd.	Urticaceae	puaket
Prosaptia alata (Blume) H.Christ	Polypodiaceae	
Psychotria sp.1	Rubiaceae	kempeniel [fluffy one]
Psychotria sp.2	Rubiaceae	kempeniel [smooth one]
Pteris quadriaurita Retz. [=Pteris 1]	Polypodiaceae	peipei
Pteris tripartita Sw. [=Pteris 2]	Polypodiaceae	
Schizaea dichotoma (L.) Sm.	Schizaeaceae	
Selaginella kanehirae Alston	Selaginellaceae	kidien mal
Sphaerostephanos heterocarpus (Blume) Holttum	Polypodiaceae	mahrek
Syzygium carolinensis (Koidz.) Hosok. [=Syzygium]	Myrtaceae	kehnpap
Syzygium stelechantha (Diels) Glassman [=Syzygium 2]	Myrtaceae	kirek en wel
Tapendidium carolinense Kramer	Polypodiaceae	peipei aramass
Tectaria crenata Cav.	Polypodiaceae	
Timonius sp.	Rubiaceae	kenmant [fluffy one]
Trichomanes javanicum var. *boryanum* (Kunze) Fosberg	Hymenophyllaceae	
Vittaria angustifolia Blume	Polypodiaceae	
?		aiaw [vine]
?		adohl en wel [vine]
?		kehtol
?	Flacourtiaceae?	[looks like] Ngi
?		[unknown fern]
?		[Unknown vine]

Appendix B: Life-form, origin, and seed-mass characteristics of tree and shrub species

Note: for definitions of seed-mass groups and life-forms, see analysis methods, section 5.3.
Abbreviations: Life-forms: LT=large-tree species, MT=medium-tree spp., ST=small-tree spp., S=shrub spp.; Origin: E= endemic, N=native, I=introduced (origins are probable only)

Species	Life-form	Origin	Mean seed-mass (g)	Seed-mass group
Parinari	LT	N	40.8633	1
Barringtonia	ST	N	30.3946	1
Myristica	LT	N	12.7933	1
Cinnamomum	MT	E	0.9145	2
Syzygium	MT	N	0.6138	2
Clinostigma	LT	E	0.5721	2
Aglaia	ST	E	0.4742	2
Elaeocarpus	LT	N	0.3428	2
Discocalyx	S	E	0.2686	2
Palaquium	MT	E	0.2175	2
Pandanus	ST	N	0.2000	2
Flacourtia	ST	N	0.1275	2
Garcinia	MT	E	0.1000	2
Canthium	ST	E	0.0645	3
Cananga	ST	I	0.0476	3
Macaranga	ST	E	0.0258	3
Embelia	S	N	0.0255	3
Campnosperma	LT	N	0.0238	3
Glochidion	S	N	0.0204	3
Morinda	ST	N/I	0.0149	3
Premna	ST	N	0.0122	3
Timonius	MT	E	0.0117	3
Hibiscus	ST	N	0.0109	3
Pittosporum	ST	N	0.0074	3
Syzygium 2	ST	N	0.0067	3
"kehtol"	ST	N	0.0034	3
Glochidion 2	ST	N	0.0008	4
Gynotroches	MT	N	0.0007	4
Claoxylon	ST	E	0.0005	4
Fagraea	ST	N	0.0005	4
Ficus	ST	N	0.0003	4
"ngilooklike"	ST	N	0.0003	4
Maesa	ST	N	0.0001	4
Melastoma	S	N	0.0000	4
Cyathea	ST	E	0.0000	4
Psychotria 1	S	E	0.0000	?
Psychotria 2	S	E	0.0000	?
Ixora	ST	N	0.0000	?
Piper 2	S	I	0.0000	?

Appendix C: Changes in stem frequencies by plot type and species

Frequencies have been standardised to equal areas (100 quadrats).

Mature-phase forest	TIME 0	TIME 1			TIME 2			TIME 3		
SPECIES	Present	Dead	New	Present	Dead	New	Present	Dead	New	Present
Aglaia ponapensis Kaneh.	222	26	4	200	11	3	192	13	54	233
Barringtonia racemosa (L.) Spreng.	7	0	0	7	0	0	7	0	0	7
Campnosperma brevipetiolata Volkens	44	43	4	5	3	14	16	14	52	54
Canthium barbatum (G.Forst.) Seem.	3	0	0	3	0	0	3	0	1	4
Cinnamomum carolinense Koidz.	1	0	0	1	0	0	1	0	0	1
Clinostigma ponapensis (Becc.) Moore & Fosberg	203	118	4	89	29	8	68	15	54	107
Cyathea nigricans Mett.	28	2	0	25	6	1	20	1	1	20
Discocalyx ponapensis Mez	14	1	1	14	0	1	16	1	1	17
Elaeocarpus carolinensis Koidz.	1	1	0	1	0	0	1	0	1	1
Embelia palauensis Mez	19	1	2	20	1	6	25	7	3	22
Fagraea berteria var. *sair* (Gilg & Benedict) Fosberg	1	1	0	0	0	0	0	0	1	1
Ficus tinctoria G. Forst.	9	1	1	8	1	0	7	0	0	7
Flacourtia rukum var. *micronesica* Fosberg & Sachet	1	0	0	1	0	0	1	0	0	1
Garcinia ponapensis Lauterb.	6	0	0	6	0	0	6	1	1	7
Glochidion marianum Mull.Arg.	3	0	0	3	0	0	3	0	0	3
Gynotroches axillaris Blume	1	0	0	1	0	0	1	0	0	1
Hibiscus tiliaceus L.	1	1	0	1	0	0	1	0	0	1
Ixora caseii Hance	2	0	0	2	0	0	2	0	0	2
Melastoma malabathricum var. *marianum* (Naudin) Fosberg	1	0	0	1	0	0	1	1	0	0
Myristica insularis Kaneh.	105	20	1	86	5	1	82	23	38	96
Palaquium karrak Kaneh.	27	2	1	25	2	0	23	1	9	31
Pandanus cominsii var. *micronesicus* B.C.Stone	20	1	0	20	0	0	20	0	2	22
Parinari laurina Gray	675	80	14	610	33	6	583	74	115	624
Pittosporum ferrugineum W.T.Aiton	0	0	0	0	0	0	0	0	1	1
Premna obtusifolia R.Br.	0	0	0	0	0	0	0	0	1	1
Syzygium carolinensis (Koidz.) Hosok.	30	4	3	30	7	2	25	4	16	37
Syzygium stelechantha (Diels) Glassman	1	0	0	1	0	0	1	0	0	1
"NGILOOKLIKE"	2	0	0	2	0	0	2	0	0	2
	1428	301	35	1162	98	42	1107	154	351	1304

Gap-phase forest SPECIES	TIME 0 Present	TIME 1 Dead	TIME 1 New	TIME 1 Present	TIME 2 Dead	TIME 2 New	TIME 2 Present	TIME 3 Dead	TIME 3 New	TIME 3 Present
Aglaia ponapensis Kaneh.	262	25	9	246	14	6	238	42	80	276
Barringtonia racemosa (L.) Spreng.	4	1	0	3	1	0	3	0	0	3
Campnosperma brevipetiolata Volkens	58	55	8	11	8	44	46	40	174	180
Cananga odorata (Lam.) Hook.f. & Thomson	0	0	0	0	0	0	0	0	2	2
Claoxylon carolinianum Pax & Hoffman	2	0	0	2	0	0	2	0	0	2
Clinostigma ponapensis (Becc.) Moore & Fosberg	329	185	30	175	56	11	129	45	87	171
Cyathea nigricans Mett.	20	3	0	17	3	0	14	1	0	13
Discocalyx ponapensis Mez	1	0	0	1	0	0	1	0	0	1
Elaeocarpus carolinensis Koidz.	1	0	0	1	0	1	2	0	1	3
Embelia palauensis Mez	23	1	3	24	1	1	24	5	5	24
Ficus tinctoria G. Forst.	0	0	0	0	0	1	1	0	2	3
Garcinia ponapensis Lauterb.	2	0	0	2	0	0	2	0	0	2
Glochidion marianum Mull.Arg.	1	0	0	1	0	0	1	0	1	2
Ixora caseii Hance	1	0	0	1	0	0	1	0	1	2
Macaranga carolinensis var. *grandiflora* Pax & Hoffman	0	0	0	0	0	0	0	0	1	1
Myristica insularis Kaneh.	66	13	0	53	14	1	39	10	24	54
Palaquium karrak Kaneh.	13	0	0	13	0	0	13	1	3	14
Pandanus cominsii var. *micronesicus* B.C.Stone	31	0	1	32	0	0	32	3	1	30
Parinari laurina Gray	585	53	16	548	23	12	537	86	113	564
Pittosporum ferrugineum W.T.Aiton	0	0	0	0	0	0	0	0	3	3
Psychotria sp. 1	1	0	0	1	0	0	1	0	0	1
Syzygium carolinensis (Koidz.) Hosok.	26	2	1	25	1	1	25	3	7	29
Timonius sp.	1	0	0	1	0	0	1	0	0	1
"KEHTOL"	1	0	0	1	0	0	1	0	0	1
	1426	338	68	1156	121	76	1112	236	502	1377

Sakau-agro forest	TIME 0	TIME 1			TIME 2			TIME 3		
SPECIES	**Present**	**Dead**	**New**	**Present**	**Dead**	**New**	**Present**	**Dead**	**New**	**Present**
Aglaia ponapensis Kaneh.	99			99	6	6	99	15	29	114
Barringtonia racemosa (L.) Spreng.	18			18	0	0	18	1	1	18
Campnosperma brevipetiolata Volkens	122			122	35	65	151	82	69	138
Cananga odorata (Lam.) Hook.f. & Thomson	10			10	0	0	10	2	0	8
Canthium barbatum (G.Forst.) Seem.	1			1	0	0	1	0	0	1
Claoxylon carolinianum Pax & Hoffman	7			7	1	0	6	1	0	5
Clinostigma ponapensis (Becc.) Moore & Fosberg	30			30	2	1	29	7	8	30
Cyathea nigricans Mett.	113			113	14	10	109	14	25	121
Elaeocarpus carolinensis Koidz.	3			3	0	0	3	1	0	2
Embelia palauensis Mez	10			10	1	1	10	1	0	9
Fagraea berteria var. *sair* (Gilg & Benedict) Fosberg	13			13	4	1	9	5	2	6
Ficus tinctoria G. Forst.	14			14	1	1	14	2	1	13
Glochidion marianum Mull.Arg.	1			1	0	0	1	0	0	1
Glochidion ramiflorum G.Forst.	1			1	0	0	1	0	0	1
Hibiscus tiliaceus L.	2			2	0	0	2	0	0	2
Ixora caseii Hance	0			0	0	0	0	0	0	0
Macaranga carolinensis var. *grandiflora* Pax & Hoffman	8			8	0	0	8	2	0	6
Maesa carolinensis Mez	1			1	0	0	1	0	1	2
Melastoma malabathricum var. *marianum* (Naudin) Fosberg	114			114	11	2	104	46	24	82
Morinda citrifolia L. var. *citrifolia*	22			22	0	2	24	3	2	23
Myristica insularis Kaneh.	10			10	2	2	10	3	6	14
Pandanus cominsii var. *micronesicus* B.C.Stone	18			18	0	0	18	1	7	24
Parinari laurina Gray	39			39	0	0	39	2	4	41
Piper methysticum G.Forst.	3			3	0	0	3	3	1	1
Pittosporum ferrugineum W.T.Aiton	3			3	0	2	5	0	0	5
Premna obtusifolia R.Br.	2			2	0	2	4	0	1	5
Psychotria sp. 1	11			11	1	1	11	1	2	13
Psychotria sp. 2	0			0	0	0	0	0	1	1
Syzygium stelechantha (Diels) Glassman	1			1	0	0	1	0	0	1
Timonius sp.	3			3	1	0	2	0	0	2
Total	679			679	80	97	696	193	185	689

Appendix D Relative abundance of the ten most numerous woody species among plot types, time 0 cohort vs. new recruits.

Percentages are the % contribution to the total frequency. Standardised frequencies are in brackets.

	Mature-phase forest			Gap-phase forest				Sakau-agro-forest		
	Saplings at time 0	Seedlings at time 0	New recruits	Saplings at time 0	Seedlings at time 0	New recruits		Saplings at time 0	Seedlings at time 0	New recruits
Seed-mass group:							**Seed-mass group**			
1	68.5 % (150)	53.8 % (617)	41.4 % (175)	56.8 % (92)	45.2 % (550)	25.7 % (166)	1	9.4 % (19)	10.1 % (46)	5.2 % (11)
2	26.5 % (58)	38.1 % (437)	38.4 % (162)	39.1 % (63)	46.9 % (571)	36.5 % (235)	2	12.0 % (24)	26.0 % (118)	17.5 % (39)
3	2.0 % (4)	5.7 % (65)	19.7 % (83)	0	6.6 % (80)	37.3 % (240)	3	28.6 % (57)	26.0 % (118)	64.6 % (143)
4	3.0 % (7)	2.4 % (28)	0.5 % (2)	4.2 % (7)	1.3 % (16)	0.5 % (3)	4	50.0 % (100)	37.8 % (171)	12.7 % (28)
Species:							**Species**			
Parinari	62.3 % (136)	45.6 % (522)	32.0 % (136)	52.6 % (85)	40.3 % (491)	21.8 % (140)	Campnosperma	25.0 % (50)	14.5 % (66)	60.4 % (133)
Clinostigma	9.3 % (20)	14.1 % (162)	14.9 % (63)	13.0 % (21)	23.5 % (287)	19.6 % (126)	*Melastoma*	19.8 % (40)	16.4 % (74)	1.9 % (4)
Aglaia	8.3 % (18)	17.6 % (201)	14.6 % (62)	14.6 % (24)	19.3 % (234)	14.7 % (95)	*Cyathea*	27.1 % (54)	12.0 % (54)	5.7 % (13)
Myristica	3.6 % (8)	8.2 % (94)	9.4 % (40)	3.1 % (5)	4.8 % (58)	3.9 % (25)	*Aglaia*	6.3 % (13)	19.0 % (86)	16.0 % (35)
Campnosperma	(0)	3.8 % (43)	16.4 % (70)	(0)	4.6 % (56)	35.1 % (226)	*Parinari*	7.8 % (16)	5.1 % (23)	1.4 % (3)
Syzygium	(1)	2.5 % (29)	5.0 % (21)	0.5 % (1)	2.0 % (24)	1.3 % (8)	*Clinostigma*	2.6 % (5)	3.7 % (17)	(1)
Pandanus	4.3 % (9)	0.9 % (10)	(1)	9.9 % (16)	1.1 % (13)	0.3 % (2)	*Morinda*	(0)	4.8 % (22)	1.9 % (4)
Cyathea	2.6 % (6)	1.3 % (14)	(1)	3.6 % (6)	1.1 % (13)	(0)	*Pandanus*	3.1 % (6)	2.5 % (11)	0.9 % (2)
Embelia	-	1.6 % (19)	2.6 % (11)	-	1.9 % (23)	1.3 % (8)	*Barringtonia*	1.6 % (3)	3.0 % (14)	(0)
Palaquium	2.3 % (5)	1.8 % (20)	2.2 % (9)	0.5 % (1)	0.9 % (11)	0.4 % (3)	*Ficus*	0.5 % (1)	2.5 % (11)	0.9 % (2)
Other spp.	7.3 % (16)	2.6 % (32)	2.5 % (9)	2.2 % (2)	0.5 % (8)	1.6 % (12)	Other	6.2 % (12)	16.5 % (74)	10.9 % (24)
Total	(219)	(1146)	(423)	(161)	(1218)	(645)	Total	(200)	(452)	(221)

Appendix E: Species ranks among plot types for the 20 most widely present species at time 0 and 15 months

	MPF: TIME 0		MPF: 15 months		GPF: TIME 0		GPF: 15 months		SAF: TIME 0		SAF: 15 months	
Species rank	Species	% quadrats	Species	% quadrats	Species	% quads	Species	% quads	Species	% quads	Species	% quads
1	*Parinari*	72.46	*Aglaia*	73.19	*Parinari*	83.19	*Parinari*	84.87	*Nephrolepis*	81.25	*Nephrolepis*	83.33
2	*Aglaia*	68.12	*Parinari*	71.74	*Aglaia*	70.59	*Aglaia*	71.43	*Piper*	52.08	*Piper*	52.08
3	*Clinostigma*	59.42	*Pachygone*	52.17	*Clinostigma*	65.55	*Pachygone*	65.55	*Sphaerostephanos*	50.00	*Sphaerostephanos*	51.04
4	*Pachygone*	43.48	*Clinostigma*	47.10	*Pachygone*	51.26	*Clinostigma*	54.62	*Cyathea*	45.83	*Cyathea*	48.96
5	*Freycinetia*	43.48	*Freycinetia*	39.13	*Freycinetia*	47.06	*Campnosperma*	52.94	*Eragrostis*	44.79	*Eragrostis*	48.96
6	*Myristica*	39.86	*Myristica*	39.13	*Piper*	31.93	*Freycinetia*	44.54	*Campnosperma*	42.71	*Aglaia*	47.92
7	*Campnosperma*	34.06	*Campnosperma*	34.06	*Campnosperma*	31.09	*Piper*	31.09	*Aglaia*	40.63	*Campnosperma*	45.83
8	*Piper*	33.33	*Piper*	31.88	*Myristica*	29.41	*Myristica*	27.73	*Melastoma*	38.54	*Melastoma*	31.25
9	*Procris*	27.54	*Procris*	26.09	*Procris*	26.89	*Procris*	25.21	*Freycinetia*	30.21	*Hoya*	29.17
10	*Syzygium*	23.19	*Syzygium*	26.09	*Pandanus*	22.69	*Pandanus*	21.85	*Hoya*	27.08	*Freycinetia*	26.04
11	*Cyathea*	18.84	*Palaquium*	18.84	*Merremia*	19.33	*Embelia*	21.01	*Paspalum*	20.83	*Hypolytrum*	26.04
12	*Asplenium* 1	16.67	*Cyathea*	18.12	*Syzygium*	19.33	*Merremia*	20.17	"adohlenwel"	19.79	*Procris*	22.92
13	*Palaquium*	16.67	*Asplenium* 1	15.94	*Embelia*	16.81	*Syzygium*	19.33	*Hypolytrum*	18.75	*Pachygone*	20.83
14	*Merremia*	15.94	*Embelia*	15.94	*Dendrobium spp.*	15.97	*Dendrobium spp.*	15.13	*Merremia*	17.71	*Merremia*	18.75
15	*Embelia*	14.49	*Merremia*	15.94	*Asplenium* 1	15.13	*Asplenium* 2	14.29	*Pteris* 1	16.67	*Pteris* 1	18.75
16	*Hoya*	13.04	*Pandanus*	15.22	*Asplenium* 2	14.29	*Asplenium* 1	14.29	*Pachygone*	15.63	"adohlenwel"	16.67
17	*Linsaea* 1	13.04	*Hoya*	13.04	*Hoya*	14.29	*Hoya*	14.29	*Pandanus*	15.63	*Pandanus*	16.67
18	*Pandanus*	13.04	*Linsaea* 1	11.59	*Cyathea*	13.45	*Cyathea*	10.92	*Clinostigma*	12.50	*Paspalum*	16.67
19	*Vittaria*	10.14	*Vittaria*	10.14	*Linsaea* 1	10.08	*Linsaea* 1	10.08	*Ficus*	11.46	*Clinostigma*	14.58
20	*Asplenium* 2	8.70	*Asplenium* 2	7.25	*Asplenium* 3	9.24	*Asplenium* 3	9.24	*Morinda*	10.42	*Morinda*	11.46

Appendix F: Absolute and proportional seedling height growth 0-3 and 3-15 months

	0-3 mo			3-15 mo		
	MPF	GPF	SAF	MPF	GPF	SAF
All species:						
Absolute height growth (m)	0.02 ± 0.00	0.02 ± 0.01	0.04 ± 0.01	-0.02 ± 0.01	0.01 ± 0.01	0.13 ± 0.03
Proportional height growth	0.09 ± 0.01	0.14 ± 0.04	0.14 ± 0.05	0.01 ± 0.01	0.08 ± 0.03	0.31 ± 0.07
Seed-group 1:						
Absolute growth (m)	0.03 ± 0.00	0.02 ± 0.01	0.05 ± 0.01	-0.03 ± 0.01	-0.01 ± 0.01	0.04 ± 0.02
Proportional growth	0.11 ± 0.01	0.18 ± 0.07	0.10 ± 0.04	-0.03 ± 0.01	0.02 ± 0.02	0.09 ± 0.06
Seed-group 2:						
Absolute growth (m)	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.01	0.00 ± 0.01	0.03 ± 0.01	0.07 ± 0.02
Proportional growth	0.08 ± 0.02	0.10 ± 0.02	0.06 ± 0.04	0.03 ± 0.02	0.13 ± 0.04	0.19 ± 0.06
Seed-group 3:						
Absolute growth (m)	-0.03 ± 0.02	0.00 ± 0.01	0.02 ± 0.04	-0.01 ± 0.03	0.00 ± 0.01	0.11 ± 0.04
Proportional growth	-0.02 ± 0.05	0.05 ± 0.03	0.09 ± 0.10	0.02 ± 0.07	0.04 ± 0.05	0.44 ± 0.16
Seed-group 4:						
Absolute growth (m)	0.00 ± 0.01	-0.02 ± 0.00	0.03 ± 0.04	0.02 ± 0.07	0.13 ± 0.03	0.26 ± 0.12
Proportional growth	-0.05 ± 0.06	0.23 ± 0.29	0.20 ± 0.13	0.23 ± 0.19	0.60 ± 0.24	0.47 ± 0.22
Parinari:						
Absolute growth (m)	0.03 ± 0.01	0.02 ± 0.01	0.09 ± 0.02	-0.03 ± 0.01	-0.01 ± 0.02	0.02 ± 0.03
Proportional growth	0.12 ± 0.02	0.19 ± 0.07	0.14 ± 0.01	-0.04 ± 0.01	0.02 ± 0.02	0.03 ± 0.04
Clinostigma:						
Absolute growth (m)	0.05 ± 0.06	0.07 ± 0.08	0.05 ± 0.03	-0.01 ± 0.04	0.17 ± 0.11	-0.02 ± 0.04
Proportional growth	0.10 ± 0.11	0.24 ± 0.12	0.09 ± 0.01	0.10 ± 0.15	0.24 ± 0.17	0.00 ± 0.05

Appendix G: Positive seedling proportional height growth 0-15 months, by plot type

Height growth was averaged after first deleting all individuals recording negative height growth. Means with different letters are significantly different in an LSD test with α=0.01. N= 7, 6, and 5 plots for MPF, GPF, and SAF, respectively, unless otherwise stated.

	MPF	GPF	SAF	ANOVA test statistics
All species combined:	0.27 ± 0.02	0.42 ± 0.07	0.78 ± 0.25	MPF vs. GPF: F=4.41, p=0.0597 All: F=4.07, p=0.0387
Life-form:				
Large (and medium)-tree species	0.26 ± 0.03	0.51 ± 0.14	0.39 ± 0.18	MPF vs. GPF: F=3.70, p=0.0808 All: F=1.18, p=0.3330
Small-tree and shrub spp.	0.31 ± 0.04	0.38 ± 0.03	1.00 ± 0.43	MPF vs. GPF: F=1.88,p=0.1974 All: F=3.16, p=0.0715
Seed-mass group:				
1 (x ≥ 1.0 g)	0.27 ± 0.03	0.51 ± 0.15	0.24 ± 0.07	MPF vs. GPF: F=3.05, p=0.1088 All: F=2.53, p=0.1131
2 (0.1 g ≤ x < 1.0 g)	0.26 ± 0.02	0.36 ± 0.03	0.34 ± 0.04	MPF vs. GPF: F=6.38, p=0.0281 All: F=2.78, p=0.0941
3 (0.001 g ≤ x < 0.1 g)	0.23 ± 0.05 (n=5)	0.19 ± 0.06	0.83 ± 0.29 (n=4)	MPF vs. GPF: F=0.27, p=0.6175 All: F=5.79, p=0.0174
4 (x < 0.001 g)	0.91 ± 0.30 (n=4)	0.96 ± 0.41 (n=4)	1.53 ± 0.75 (n=5)	MPF vs. GPF: F=0.01, p=0.9157 All: F=0.38, p=0.6964
Species:				
Parinari	0.26 ± 0.04 (n=7)	0.54 ± 0.15 (n=6)	0.23 ± 0.09 (n=2)	MPF vs. GPF: F=3.80, p=0.0772 All: F=2.35, p=0.1373
Aglaia	0.23 ± 0.02	0.38 ± 0.05	0.32 ± 0.05	MPF vs. GPF: F=8.11, p=0.0159 All: F=3.52, p=0.0557
Clinostigma	0.41 ± 0.15 (n=4)	0.73 ± 0.24 (n=6)	0.30 ± 0.28 (n=2)	MPF vs. GPF: F=1.03, p=0.3390 All: F=0.87, p=0.4499
Campnosperma	.	.	0.95 ± 0.23 (n=3)	.

Appendix H: Maximum seedling proportional height growth 0-15 months, by plot type

Data were averaged from the individual in each species(group) with the greatest height growth record per quadrat. Means with different letters are significantly different in an LSD test with α=0.01. N= 7, 6, and 5 plots for MPF, GPF, and SAF, respectively, unless otherwise stated.

	MPF	GPF	SAF	ANOVA test statistics
All species combined:	0.78 ± 0.13	0.98 ± 0.09	1.47 ± 0.50	MPF vs. GPF: F=1.38, p=0.2650 All: F=1.75, p=0.2077
Life-form:				
Large (and medium)-tree species	0.66 ± 0.16	0.88 ± 0.11	0.51 ± 0.23	MPF vs. GPF: F=1.20, p=0.2964 All: F=1.19, p=0.3327
Small-tree and shrub spp.	0.49 ± 0.05	0.61 ± 0.05	1.67 ± 0.71	MPF vs. GPF: F=2.90,p=0.1164 All: F=3.43, p=0.0591
Seed-mass group:				
1 (x ≥ 1.0 g)	0.67 ± 0.16	0.89 ± 0.15	0.34 ± 0.14	MPF vs. GPF: F=0.99, p=0.3408 All: F=2.89, p=0.0866
2 (0.1 g ≤ x < 1.0 g)	0.41 ± 0.04	0.58 ± 0.04	0.43 ± 0.05	MPF vs. GPF: F=8.89, p=0.0125 All: F=4.36, p=0.0321
3 (0.001 g ≤ x < 0.1 g)	0.24 ± 0.05 (n=5)	0.19 ± 0.06	0.96 ± 0.35 (n=4)	MPF vs. GPF: F=0.38, p=0.5535 All: F=6.10, p=0.0149
4 (x < 0.001 g)	1.17 ± 0.38 a (n=4)	1.10 ± 0.44 a (n=4)	2.33 ± 1.30 b (n=5)	MPF vs. GPF: F=0.01, p=0.9095 All: F=0.59, p=0.5744

Appendix I: Seedling height growth 3-15 months among recruitment cohorts

HGT315=absolute height growth 3-15 months, RHGT315=proportional height growth 3-15 months. Means with different letters are significantly different in ANOVA and associated LSD tests with p<0.01.

	MPF		GPF		SAF	
	HGT315	RHGT315	HGT315	RHGT315	HGT315	RHGT315
All species:						
Time 0 cohort	-0.01 ± 0.01 a	0.01±0.01 a	0.01 v 0.01a	0.08 ± 0.03 a	0.12 ±0.02b	0.31 ± 0.06 b
1-month cohort	0.05±0.03	0.13 ± 0.03	0.13 ± 0.04	0.51 ± 0.25	.	.
3-month cohort	0.05 ± 0.06	0.34 ± 0.37	0.12 ± 0.02	1.07 ± 0.34	0.35 ± 0.30	1.28 ± 0.77
Seed-group 1:						
Time 0 cohort	-0.02 ± 0.01 a	-0.03 ± 0.01	-0.01 ±0.02ab	0.02 ± 0.02	0.04 ± 0.02 b	0.09 ± 0.06
1-month cohort	0.07 ± 0.03	0.16 ± 0.05	0.21 ± 0.04	0.72 ± 0.35	.	.
3-month cohort	0.09 ± 0.10	0.56 ± 0.62	0.20 ± 0.04	1.25 ± 0.68	.	.
Seed-group 2:						
Time 0 cohort	-0.00 ± 0.01 a	0.03 ± 0.02 a	0.03 ± 0.01ab	0.13 ± 0.04ab	0.06 ± 0.01 b	0.18 ± 0.04 b
1-month cohort	0.01 ± 0.00	0.14 ± 0.06	0.01 ± 0.01	0.07 ± 0.09	.	.
3-month cohort	-0.02 ± 0.04	0.02 ± 0.48	0.07 ± 0.02	0.72 ± 0.24	0.03 ± 0.02	0.39 ± 0.33
Seed-group 3:						
Time 0 cohort	-0.01 ± 0.03	0.03 ± 0.07 a	0.00 ± 0.01	0.04 ± 0.05 a	0.09 ± 0.05	0.43 ± 0.17 b
1-month cohort	-0.03 ± 0.03	-0.13 ± 0.08	0.03 ± .	0.43 ± .	.	.
3-month cohort	0.0 a	0.0 a	0.04 ± 0.00 b	0.87 ± 0.07 b	0.05 ± 0.02	0.89 ± 0.44
Seed-group 4:						
Time 0 cohort	0.02 ± 0.07	0.23 ± 0.19	0.13 ± 0.03	0.60 ± 0.24	0.23 ± 0.09	0.48 ± 0.21
1-month cohort	.	.	.	.	.	.
3-month cohort	.	.	0.0	0.0	0.38 ± 0.30	1.12 ± 0.82
Parinari:						
Time 0 cohort	-0.02 ± 0.01	-0.04 ± 0.01	-0.01 ± 0.02	0.03 ± 0.02	0.02 ± 0.03	0.03 ± 0.04
1-month cohort	0.07 ± 0.03	0.16 ± 0.05	0.21 ± 0.04	0.72 ± 0.35	.	.
3-month cohort	0.14 ± 0.16	0.87 ± 0.92	0.20 ± 0.04	1.25 ± 0.68	.	.

Appendix J: Mean plot height (m) at 15 months by plot-type, seed-mass group or species, and cohort.

	Mature-Phase Forest		Gap-Phase Forest		Sakau-Agro-Forest	
	Time 0 cohort	New Recruits	Time 0 cohort	New Recruits	Time 0 cohort	New Recruits
All Species combined	0.47 ± 0.04	0.22 ± 0.03	0.45 ± 0.02	0.18 ± 0.02	0.40 ± 0.04	0.11 ± 0.02
Seed-mass group						
1	0.61 ± 0.03	0.40 ± 0.02	0.61 ± 0.02	0.41 ± 0.03	0.62 ± 0.06	0.41 ± 0.15
2	0.24 ± 0.03	0.11 ± 0.01	0.24 ± 0.02	0.12 ± 0.01	0.36 ± 0.06	0.12 ± 0.01
3	0.22 ± 0.04	0.06 ± 0.01	0.21 ± 0.06	0.06 ± 0.00	0.43 ± 0.03	0.07 ± 0.01
4	0.33 ± 0.08	0.06 ± 0.01	0.43 ± 0.06	0.14 ± .	0.35 ± 0.04	0.17 ± 0.04
Species						
Parinari	0.65 ± 0.02	0.48 ± 0.05	0.63 ± 0.03	0.44 ± 0.03	0.72 ± 0.10	0.31 ± .
Aglaia	0.23 ± 0.02	0.10 ± 0.01	0.21 ± 0.02	0.11 ± 0.02	0.35 ± 0.07	0.11 ± 0.01
Clinostigma	0.39 ± 0.12	0.10 ± 0.01	0.31 ± 0.09	0.11 ± 0.01	0.41 ± .	----
Campmosperma	----	0.05 ± 0.00	----	0.06 ± 0.00	0.49 ± 0.11	0.06 ± 0.00
Cyathea	0.30 ± 0.08	0.05 ± .	0.38 ± 0.02	----	0.27 ± 0.02	0.19 ± 0.07